Stability and Structure of Model Food-webs with Adaptive Behavior

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Zusammenfassung

In dieser Arbeit wird der Einfluß adaptiven Verhaltens auf die Stabilität und Struktur von Nahrungsnetzwerken untersucht.

Als erstes behandeln wir größtenteils analytisch den Einfluß der Art der Populationsdynamik und des adaptiven Verhaltens auf die Zahl der Verknüpfungen und die Stabilität von Spezies mit kleiner Populationsgröße. Wir vergleichen Modelle mit funktioneller Reaktion vom Typ Lotka-Volterra mit Modellen mit funktioneller Reaktion vom Holling Typ II. Wir stellen Modelle mit linearer und solche mit nichtlinearer Beschränkung der Nahrungsaufnahme gegenüber und wir vergleichen Modelle mit Nahrungsauswahl mit sogenannten patch choice Modellen. Ein Ergebnis der Untersuchungen ist, dass adaptive Nahrungssuche ("adaptive foraging") immer einen stabilisierenden Effekt auf kleine Populationen hat und dass nichtlineare funktionelle Reaktionen und eine nichtlineare Beschränkung der Nahrungsaufnahme zu realistischeren Verknüpfungszahlen im Nahrungsnetz führen.

Des weiteren untersuchen wir den Einfluß der funktionellen Reaktion (Lotka-Volterra oder Holling-Typ II), der anfänglichen Topologie des Netzes (Zufallsnetz oder Nischen-Modell), der Art des adaptiven Verhaltens (adaptive Nahrungssuche versus Räubervermeidung) und der Art von Beschränkung des adaptiven Verhaltens (linear oder nichtlinear) auf die Stabilität und die Struktur von großen Nahrungsnetzen. Zwei Arten der Netzstabilität werden betrachtet: Zum einen die Robustheit des Netzwerkes (der Anteil der Spezies, die nach der Populationsdynamik überlebt), zum anderen die Stabilität gegen Auslöschung von Spezies (Überlebende Spezieszahl nach der Entfernung einer zufälligen Spezies). Wenn wir die Netzstruktur auswerten, betrachten wir die Verbindungsdichte und die Zahl der trophischen Ebenen. Wir zeigen, dass die Art der funktionellen Reaktion und die Ausgangsnetzstruktur keinen großen Effekt auf die Stabilität der Nahrungsnetze haben. Das Nahrungsauswahlverhalten (adaptive foraging) dagegen bewirkt einen großen stabilisierenden Effekt. Das führt zu einem positiven Komplexitäts-Stabilitäts-Verhältnis, wenn "Komplexität" bedeutet, dass es mehr potentielle Beute pro Spezies gibt. Eine weitere Art anpassungsfähigen Verhaltens ist die Vermeidung von Räubern. Dieses adaptive Verhalten macht Nahrungsnetze nur ein wenig stabiler. Die beobachtete Verknüpfungsdichte nach der Populationsdynamik hängt stark davon ab, ob adaptive Nahrungssuche implementiert wird. Wir zeigen auch, dass die Struktur der Netzwerke hinsichtlich der trophischen Ebenen bei Populationsdynamik mit adaptiver Nahrungssuche erhalten bleibt.

Ferner werden lokale und globale Stabilität der Fixpunkte der Lotka-Volterra Populationsdynamik mit und ohne adaptive Nahrungssuche analysiert. Wir formulieren eine Bedingung, unter der positive Fixpunkte stabil sind. Betrachtet man die lokale Stabilität, trifft diese Bedingung auf die mögliche Verbindungsstruktur für die Populationsdynamik ohne adaptive Nahrungssuche zu. Für die Populationsdynamik mit adaptiver Nahrungssuche trifft die Bedingung hingegen auf die effektive Verbindungsstruktur zu. Bei global stabilen Fixpunkten trifft die Bedingung auf die mögliche Verbindungsstruktur in beiden Fälle zu. Wir finden auch, dass intraspezifische Konkurrenz Fixpunkte stabilisiert.

Schliesslich wird die Stabilität von Netzen mit und ohne adaptiver Nahrungssuche

unter Evolution untersucht, d.h. die Widerstandsfähigkeit der Netze gegen langsame Veränderungen der Verknüpfungsmuster. Modell-Nahrungsnetze ohne adaptive Nahrungssuche sind instabil unter evolutionärer Dynamik, d.h. sie kollabieren nach einiger Zeit, unabhängig von den Details des Modells. Die resultierenden Nahrungsnetze haben nur eine trophische Ebene. Im Gegensatz dazu sind Nahrungsnetze mit adaptiver Nahrungssuche stabil unter Evolution und die resultierenden Netze haben mehr als eine trophische Ebene.

Contents

Chapter 1

Introduction

Idea of earlier ecologists The relationship between stability and complexity in food webs is one of the most challenging and practically important issues in ecology and has been discussed extensively in the ecological literature. The traditional view of ecologists, obtained by intensive field observations, was that more complex ecosystems are more stable (Voute, 1946; MacArthur, 1955). Actually a famous ecologist MacArthur believed that a community shows more stability as the number of energy transportation paths in the community increases, and he referred to the ecological diversity index which he proposed in his paper as measure of stability.

The positive relationship between stability and complexity in ecological communities was first explicitly and in a general form recognized by ecologist Elton (1958). He listed evidence for his theory in the last chapter of his book (Elton, 1958; Stiling, 2002; Shimada et al., 2005):

1. Ecosystems in small, simple islands are much more vulnerable to invading species than those of continents. For example, a large extinction of birds in the Hawaiian islands has been caused by invasion and outbreaks of mosquitoes.

2. Outbreaks of pests are often found in simple cultivated land or land disturbed by humans, both of which are areas with few other naturally occurring species.

3. Tropical rain forests do not often have insect outbreaks like those common in less diverse temperate forests.

4. Pesticides have caused pest outbreaks by elimination of predators and parasites from the insect community of crop plants.

5. According to mathematical models, a system with a few species is unstable.

6. In all the simple laboratory communities constructed by two or more species, several species become extinct.

However since these original arguments were proposed, some studies have countered them (Begon et al., 1986):

1. There are many examples of introduced species invading continents and assuming pest proportions, including rabbits in Australia and pigs in North America.

2. Agricultural systems may suffer from pest outbreaks not because of their simplicity. Natural monocultures of native plants, such as "Spartina" and "Juncus", two salt marsh species, and of bracken fern seem to be stable.

3. Goodman (1975) argued that the stability of tropical ecosystems is a myth. There are reports of cases in which insects fluctuate in tropical rain forests (e.g., Wolda (1978)).

4. Pesticides do not always cause pest outbreaks, even though they remove predators and parasites from communities and make communities simple.

5. A small model system can show stability. There is no evidence that the systems size brings stability.

6. It is true that species in a small laboratory community tend to become extinct. But we cannot conclude that large laboratory communities could be more stable. There are laboratory experiments which show that larger laboratory communities are less stable than smaller laboratory communities (e.g., Luckinbill (1979)).

Of course at this stage it was not clearly defined what stability and complexity meant.

Classical theoretical results The first theoretical investigation of this issue, which was the next major step in the stability-complexity debate, was made numerically by Gardner and Ashby (1970) and analytically by May (1972) with a precise definition of stability and complexity. They investigated randomly linked model food webs with Lotka-Volterra dynamics, and looked for (linearly) stable fixed points of the dynamics. May found that food webs are likely to be stable (i.e., the food web dynamics has a stable fixed point with all population sizes being positive) only if the inequality

$$a(SC)^{1/2} < 1 \tag{1.1}$$

is satisfied. Here a is the (average) interaction strength between species, S the number of species and C is the connectance, i.e., the probability that two species in a community are in a prey-predator relation. That is, according to his theory, food webs containing more species or more or stronger links are less stable. Since more species or more links imply a higher complexity, this theoretical result is in contradiction with the idea of old field ecologists. Because this result was so surprising, many food web models based on Lotka-Volterra dynamics were further studied, but the main results were similar to what May had obtained (Kobayashi, 1980; 1986). Together with the counterarguments listed above, the conclusion of the model study was so critical to allow a number of ecologists to think of the possibility of negative stability-complexity relations in ecosystems.

But on the other hand, it has been also noted that real food webs have features that are ignored in randomly linked Lotka-Volterra-type models. For instance, McNaughton (1977) and Rejmánek and Starý (1979) reported that the system size S and connectance C are not independent but negatively correlate. It is also known that the distribution and strength of links in real food webs are far from random (Solé and Montoya, 2001; Dunne et al., 2002). And there have been proposed and studied more realistic models that use link values taken from real food webs (Yodzis, 1981), or that assemble a food web by repeated addition of species from a large species pool that contains different types of species ("plants", "herbivores", "carnivores", "top predators") (Law, 1999; Morton and Law, 1997), arriving thus at large stable food webs. Additionally, in a study using another type of dynamics than Lotka-Volterra dynamics, called Holling type-II dynamics, it has been found that the presence of many weak links stabilizes the dynamics of small food web modules by reducing population fluctuations (McCann et al., 1998). Furthermore adaptive behavior of species (adaptive foraging or predator avoidance) is also one of the important factors that were not included in the old model food webs, whose effects on stability and structure of webs are investigated in this dissertation in detail.

Adaptive foraging and predator avoidance Many species show adaptive behavior in the way they forage for prey or avoid predators. Adaptive behavior of individuals allows a species to increase its growth rate by assigning more time or effort to searching for the more profitable prey or to avoiding dangerous predators (Alexander, 1996; McNamara et al., 2001; Sih and Christensen, 2001). As the total time or energy available to a species is limited, the adaptive dynamics happens under the constraint that the total time or energy invested in the different activities remains constant. This is usually modeled by introducing a parameter, which we call "effort" in this dissertation, that is associated with each link of a species. It represents the fraction of time or energy devoted to this link, and it is therefore normalized to 1 for each species. The effort into links that yield more gain per unit effort is increased. For fixed populations sizes, this usually leads to a fixed point of the adaptive dynamics, which is a Nash equilibrium in the language of game theory (Hofbauer and Sigmund, 1998). If the time scale of the population dynamics is not much slower than that of adaptive dynamics, complex dynamical behavior may arise. This was pointed out by Abrams and Matsuda (2004), who realized the importance of the time lag in the response of predator preference to changes in prey density.

A predator searching for one prey may at the same time encounter another prey that requires a similar search strategy. For this reason, the condition that the different efforts of one species add up to 1 is not always realistic. This is usually taken into account by grouping species that are searched for simultaneously into "prey trophic species" (Matsuda and Namba, 1991), as if they constituted a single food item. Alternative approaches that also consider the intermediate case of partial overlap between search strategies for different predators have not been suggested so far.

Adaptive behavior has been implemented in different ways. It has been used in

combination with Lotka-Volterra and Holling type II dynamics, and with growth terms that are linear or nonlinear in the prey consumption rate. Different prey species may be well mixed in space, or confined to different patches. Predator avoidance can be predator-specific, unspecific, or not included at all. In the case of Holling type II dynamics, the effort is by some authors multiplied with the functional response, and by other authors it is multiplied with the encounter rate. All these variations will affect the possible number of links that can be realized at fixed points of the dynamics. This has been shown for the case of nonspecific predator avoidance versus specific predator avoidance by Matsuda et al. (1994). However, there exists not yet a systematic study of the effect of these different variations.

Stability concepts Local stability of a fixed point is just one of the definitions of stability and we can find various stability concepts and definitions in ecological literature. Grimm and Wissel (1997) found 163 different stability definitions by reviewing ecological papers and books and classified them into 6 categories (A similar classification can be found in Pimm (2002)):

1. Constancy: staying essentially unchanged.
2. Resilience: returning to the reference state after a temporary disturbance.
3. Persistence: persistence through time of an ecological system.
4. Resistance: staying essentially unchanged despite the presence of disturbances.
5. Elasticity: speed of return to the reference state after a temporary disturbance.
6. Domain of attraction: the whole of states from which the reference state can be reached again after a temporary disturbance.

In this dissertation, the following stabilities are investigated:

- Persistence of a species with a small population size : chapter 2.
- Robustness: community persistence, i.e., the percentage of species surviving under population dynamics starting from some initial state (Kondoh, 2003, 2006; Brose et al., 2003) : chapter 3.
- Species deletion stability: persistence of a community after the deletion of a randomly chosen species (Pimm, 2002) : chapter 3.
- Local stability of fixed points (Quirk and Ruppert, 1965; Gardner and Ashby, 1970; May, 1972; Jefferies, 1974) : chapter 4.
- Global stability of fixed points (Takeuchi, 1996) : chapter 4.
- Stability under evolution: persistence and resistance under long-term changes of linkage patterns of a web due to mutation or speciation of species (Caldarelli et al., 1998; Drossel et al., 2001; Bastolla et al., 2001; Bastolla et al., 2002; Drossel et al., 2004) : chapter 5.

In the subsequent paragraphs, giving the background of these stabilities, we describe what are the main purposes of the following chapters of this dissertation.

Systematic introduction of models In chapter 2, we introduce food web models with adaptive behavior and at the same time fill the above mentioned gaps by investigating mainly analytically the influence of the precise implementation of population dynamics and of adaptive behavior on the structure (e.g., the number of links) in a food web and on the stability of species with a small population size. In contrast to most other authors, we perform analytical calculations on larger food webs consisting of several trophic levels. Where such calculations are not possible, we perform computer simulations on small networks. We study systems with Lotka-Volterra and Holling type II functional response, without and with predator avoidance, without and with prey being distributed in different patches, and with linear and nonlinear constraints on efforts. We find that for Lotka-Volterra population dynamics and linear constraints on the efforts, the possible link numbers are very restricted, while we do not find such constraints in nonlinear equation systems. Nonlinear terms are also necessary if nontrivial predator avoidance behavior shall emerge. Since nonlinear terms appear to be more realistic, this finding fits well together with the empirically found large link numbers in large food webs.

There we also find that for any type of adaptive foraging, species with small population sizes can survive irrespective of the number and strength of their predators, as long as they have enough food to compensate for the natural death rate and as they are not the only prey of their predator. This finding is satisfactory as adaptive behavior has been shown to stabilize food web dynamics in various ways. The results discussed in chapter 2 have been published in Uchida et al., (2007).

Effects of adaptive behavior on persistence Adaptive behavior must affect the population dynamics and the food web persistence and structure in several ways, and in recent years various publications were devoted to this topic. Thus analytical and numerical investigations of models of predator-prey systems have shown that adaptive behavior can promote the coexistence of competing consumers (Křivan, 2003) as well as of competing prey (Křivan and Eisner, 2003). Furthermore, adaptive behavior was shown to affect the link-species relationship (Matsuda and Namba, 1991; Matsuda et al., 1994; Matsuda et al., 1996) and to promote the persistence of species (van Baalen et al., 2001).

It was also suggested that adaptive behavior of consumers is very efficient at stabilizing large complex webs and can lead to a positive stability-complexity relationship (Genkai-Kato and Yamamura, 1999; Genkai-Kato and Yamamura, 2000; Kondoh, 2003). Many species are capable of choosing how much effort they spend on each type of foraging activity. Kondoh (2003) included adaptive dynamics of the foraging efforts in the food web models and defined stability in terms of robustness. The probability that a randomly generated initial food web retains all species under combined population and adaptive dynamics was found to increase with increasing connectance, if the percentage of adaptive feeders and the speed of adaptation are sufficiently large. In contrast, Brose et al. (2003) found that if more realistic population dynamics (that is Holling type II instead of Lotka-Volterra) and more realistic web structures (i.e., niche model instead of random model or cascade model) are used, stability does not increase with complexity measured in terms of connectance. Kondoh (2006) countered this objection by showing

that the niche model has less basal species when connectance is higher, and that the positive stability-complexity relationship is recovered when food webs with the same number of basal species are evaluated.

In chapter 3, we present a more thorough study of the relationship between robustness and complexity in food web models with and without adaptive behavior, thus demonstrating the mechanism behind Kondoh's findings. We use different network models (random and niche), different population dynamics (Lotka-Volterra and Holling) and different types of adaptive behavior (adaptive foraging with linear or nonlinear constraints on the foraging efforts). In order to avoid the above-mentioned problems on external resources, we fix the number of external resources. In addition to the robustness of the food web, we evaluated the trophic structure and effective connectance of the resulting webs and their species deletion stability. Our main finding is that the most important stabilizing factor is the number of potential prey species a consumer can choose from. The content of this chapter can also be found in Uchida and Drossel (2007).

Foodweb topology and stability of fixed points The fixed point analysis of Lotka-Volterra systems by Gardner and Ashby (1970) and May (1972) related connectance with local stability of fixed points but did not take into account the influence of linkage patterns (topology) of food webs. Their conclusion is that a food web with large connectance is anyway likely to be unstable regardless of the linkage patterns. On the other hand, Quirk and Ruppert (1965) related topology of webs to local stability of fixed points for general dynamical systems by giving sufficient conditions under which the fixed point is stable, which is known as Quirk-Ruppert theorem. In chapter 4, we apply the idea of this theorem to Lotka-Volterra systems coupled to adaptive dynamics.

The original theorem says that all real parts of the eigenvalues of a Jacobi-matrix J at a fixed point of a dynamical system are negative if (i) the determinant of J is not zero, (ii) $J_{ii} \leq 0$ for all i, (iii) $J_{ii} < 0$ for at least one i, (iv) for all pairs $i \neq j$, $J_{ij}J_{ji} \leq 0$, (v) for any s-tuple with $s > 2$ constructed by different variables $(i_1 \neq i_2 \neq i_3 \cdots \neq i_{s-1} \neq i_s \neq i_1)$, the loop product $J_{i_1 i_2} J_{i_2 i_3} \cdots J_{i_{s-1} i_s} J_{i_s i_1} = 0$. A matrix J that satisfies the conditions (i)-(v) is called sign stable (Quirk and Ruppert, 1965; Jefferies, 1974). If we construct a web by saying that two variables are connected if $J_{ij}J_{ji} \neq 0$ for $i \neq j$, the condition (v) can be considered as a condition for the topology of the web and it says that the web has a tree structure (see Figure 4.1 (a). Note: the directions of links are defined by the sign of J_{ij}.).

This theorem was however proven not only for equations used in food web modeling like Lotka-Volterra systems but generally for any dynamical system therefore the special properties of ecological equations are not required to obtain the theorem. In fact, conditions (i), (ii), (iii), (iv) are clearly satisfied by Lotka-Volterra equations under normal circumstances but (v) is valid only for few Lotka-Volterra systems. The first purpose of chapter 4 is therefore to generalize the theorem (i.e., weaken the condition (v)) by restricting ourselves to considering only Lotka-Volterra systems.

A second motivation of chapter 4 is that the theorem can be directly applied only to Lotka-Volterra systems that do not include adaptive behavior (Jefferies,

1974; Zhen and Cohen, 2001; Dambacher et al., 2003) because, in that case, food webs defined using the values of J are identical to food webs the Lotka-Volterra systems describe (that is to say, $J_{ij}J_{ji} \neq 0$ implies that i and j are in predator-prey relation) if we do not include interspecific competition into the model. However we can not directly apply this theorem to systems that couple population dynamics to the dynamics for adaptive behavior because in that case not only the nodes but also all the links have dynamics and therefore we can not easily relate the webs defined by the Jacobi-matrix J of the systems to the topology of food webs. We therefore investigate the influence of adaptive foraging dynamics i.e., to know how and to what extent the foraging dynamics stabilizes the system. This allows us to learn about one side of the property of adaptive dynamics.

If we try to relate the stability of fixed points to other stability criteria like robustness discussed in chapter 3, local stability is not useful because local stability gives us information only about the stability near a fixed point. Therefore in order that a trajectory approaches the fixed point, the initial state has to be placed near the fixed point. However, because we do not know how close the initial state must be to the fixed point, it is not possible to even estimate the probability that the trajectory approaches the fixed point. Thus we can not say anything about stability in the ecological sense from the information about local stability. In the latter part of chapter 4, we investigate conditions for the global stability of fixed points. A global stability of a fixed point implies that the domain of attraction is the whole phase space. Even though there exist some results concerning the global stability of classical Lotka-Volterra systems (i.e., without adaptive dynamics) (Takeuchi, 1996), there are no results for the global stability of the Lotka-Volterra system coupled to foraging dynamics. The global stability also gives us information about dynamics of a system. Once a fixed point has turned out to be globally stable, we can exclude dynamical behavior such as periodic or chaotic behavior other than stationary behavior: all trajectories must approach the global fixed point and the system has a perfect constancy.

Evolutionary model In addition to population dynamics and adaptive dynamics, the linkage pattern and the composition of a food web also changes with time but on longer time scales (evolutionary times scales) for instance due to immigration or speciation of species. There are food web models that incorporate such longer time scales called evolutionary models. Thus evolutionary models include the successive introduction of daughter species with a small population size (i.e., a variation of an existing species called mother species) and species extinctions due to population dynamics.

The evolutionary model with population dynamics (but without adaptive dynamics) was first proposed by Caldarelli et al., (1998). The authors used very simple linear population dynamics. In this model, a species is characterized by a binary string called a feature vector, according to which the prey-predator relations in the web are determined. After the calculation of the population dynamics, a randomly chosen (surviving) species "mutates" by changing one bit in the feature vector, and as a result the web composition and linkage pattern will be changed. They reported that, starting with a small web, larger webs can be built after long

"evolutionary time" and the structure of the resulting webs are very similar to those of real food webs. In a subsequent paper by Drossel et al. (2001) it was reported that, using the same evolutionary dynamics, which is called the webworld model, large food webs are still built even when more realistic population dynamics are used.

There is another evolutionary model proposed by Lässig et al. (2001) and Bastolla et al. (2002), which uses population dynamics of conventional Lotka-Volterra type, where, in addition to prey-predator interactions, interspecific competitive interactions (i.e., competitions between different species) are taken into account. In this model, the mutations of species consist in a change of a predation link (strength of a link is modified or a daughter species obtains one more prey than mother species). In Lässig et al. (2001), the model was analyzed by mean-field approximation, and it was reported that the obtained web must have a structure similar to realistic food webs. However, the same authors showed only the results of computer simulations for a system in which all the species feed on external resources with fixed population sizes (Bastolla et al., 2002). In contrast to this, Bastolla et al. (2001) investigated the same evolutionary model without interspecific competition, and obtained food webs with several trophic levels (i.e., there are a number of species feeding on non external resources). They also reported that these web structures can be sustained under long-term changes of linkage patterns. Moreover, Drossel et al. (2004) showed that if interspecific competition is taken into account in the webworld model, it is difficult to obtain food webs having several trophic levels as long as they use the conventional population dynamics without adaptive foraging.

Therefore in chapter 5, we investigate the effects of adaptive behavior (adaptive foraging) on persistence and resistance of food webs under evolution, based on the model of Lässig et al. (2001) and Bastolla et al. (2002) including interspecific competition. The main aim is to investigate if large complex food webs are created when adaptive foraging is incorporated into the evolutionary model.

Chapter 6 summarizes the conclusions of this dissertation.

Chapter 2

Basic Properties of Models

We will introduce the basic models for population dynamics and adaptive behavior (foraging and predator avoidance) and discuss the main properties of these models. These models include also patch choice models and nonlinear constraints on the foraging efforts. In section 2.2, we investigate the stabilizing effect of adaptive foraging on small populations, and we use analytical calculations and computer simulations to find the possible number of links in the different models. Finally in section 2.3, we will compare the properties of food webs with the different versions of adaptive behavior, and we will discuss the consequences of our findings.

2.1 Population dynamics and adaptive behavior

In this section, the different types of dynamical equations used in the literature to describe population dynamics without and with adaptive behavior are presented and discussed. The consequences for the structure (possible link numbers) and the stability of the networks described by these equations will be investigated in the next section.

2.1.1 Population dynamics

The most general form of the classical population dynamics found in literature is

$$\frac{dN_i(t)}{dt} = \sum_{j\in B_i} \lambda_{ij} g_{ij}(t) N_i(t) - \sum_{k\in R_i} g_{ki}(t) N_k(t) - \alpha_i N_i(t) - \beta_i N_i^2(t), \qquad (2.1)$$

where N_i is the biomass of species number i and B_i (R_i) is the set of prey (predator) species of i. Specifying the prey set B_i or the predator set R_i for all i completely determines the topology (i.e., link structure) of food webs. The term $\lambda_{ij} g_{ij}(t) N_i(t)$ represents the energy in-flow to i due to consuming prey j, and $g_{ki}(t) N_k(t)$ the energy out-flow from i to predator k (Figure 2.1). The factor λ_{ij} in the first term is the nutritional value of an individual j for its predator i called the ecological efficiency (or energy conversion efficiency). It has to be smaller than 1, since not all food consumed is converted into predator mass. The parameter α_i is the mortality of species i. β_i measures the strength of competition within a species for necessities

other than food (intraspecific competition). We will also consider variations of this model with no direct competition term (which is a good model if predation and food limitation determine the population size), and with interspecific competition later.

The prey set B_i can include external resources on which the basal species feed, whose sizes are assumed to be constant (i.e., they do not have population dynamics.), implying that the external resources are replenished quickly and are always at their carrying capacity. External resources do not feed on any species. Thus, for basal species, the first and third term on the right-hand side of Eq. (2.1) add up to a constant and positive growth term. In this case if $E_i' = E_0 - \alpha_i$ denotes the positive growth rate with the energy in-flow from resources E_0, the last two terms result into the logistic form: $E_i' N_i - \beta_i N_i^2 = E_i'(1 - N_i/K_i)N_i$, where $K_i = E_i'/\beta_i$ is called carrying capacity.

The time dependent coefficient $g_{ij}(t)$ called functional response represents the strength of energy flow from j to one individual of species i at time t i.e., the amount of food item of prey j which one individulal of i eats in a unit time, as a function of biomass of prey N_j. The concept of the functional response was originally suggested by Solomon (1949). The simplest form of the functional response assumes that the individual predator consumes more prey as the prey biomass increases and is given by the linear form

$$g_{ij}(t) = a_{ij} N_j(t), \tag{2.2}$$

called the Lotka-Volterra type or type I functional response. Here $a_{ij} > 0$ is the coupling strength between i and j. Due to its simple form, this type of functional response has been widely recognized and is used especially in the mathematical literature.

With a type II functional response (or Holling type II functional response), the predators get eventually satiated and finally stop feeding. This situation can be

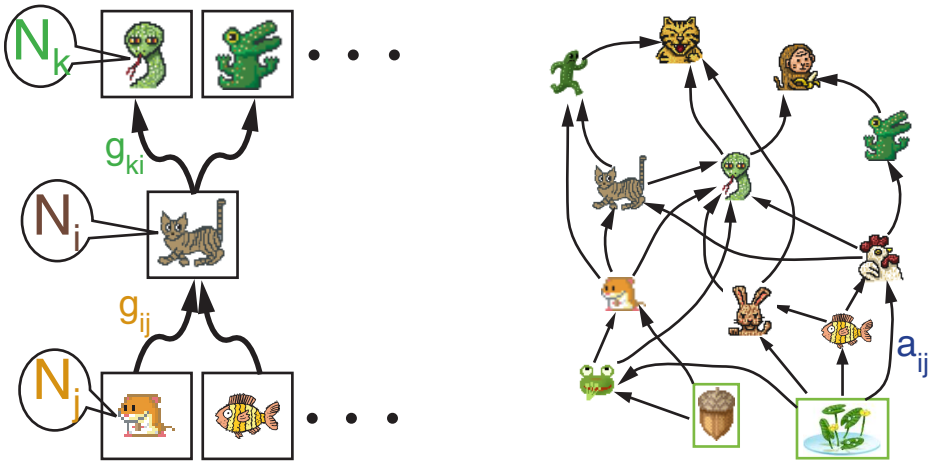


Figure 2.1: Images of energy flow and food webs.

modeled according to Arditi and Michalski (2004) by

$$g_{ij}(t) = \frac{a_{ij} N_j(t)}{1 + \sum_{j' \in B_i} h_{ij'} a_{ij'} N_{j'}(t)}, \tag{2.3}$$

which is an extension to several prey of the form originally proposed by Holling (1959b). The Holling type II functional response is the one most widely used in the modeling of food webs, since it has a mechanistic basis (Holling, 1959a; Real, 1977) and can be derived by the following simple argument: Let us denote the total searching time of a predator for its prey by T^{search}. Then the amount of prey j the predator has found during the search is proportional to biomass (or prey density) N_i of the prey and searching time T^{search}:

$$n_j = a_{ij} N_j T^{\text{search}}, \tag{2.4}$$

$$n^{\text{total}} = \sum_{j \in B_i} a_{ij} N_j T^{\text{search}}, \tag{2.5}$$

where a_{ij} is naturally interpreted as an encounter rate of prey j and predator i. Now the predator is assumed to need time to deal with the hunted prey (e.g., to kill or to eat and digest the prey). Denoting the time needed for the predator to deal with one unit of prey biomass by $h_{ij} \geq 0$, and total time by T^{total}, we find the relation

$$T^{\text{total}} = T^{\text{search}} + \sum_{j \in B_i} h_{ij} n_j, \tag{2.6}$$

which together with (2.4) yields the functional response

$$g_{ij}(N_j) = \frac{n_j}{T^{\text{total}}} = \frac{a_{ij} N_j}{1 + \sum_{j' \in B_i} h_{ij'} a_{ij'} N_{j'}}. \tag{2.7}$$

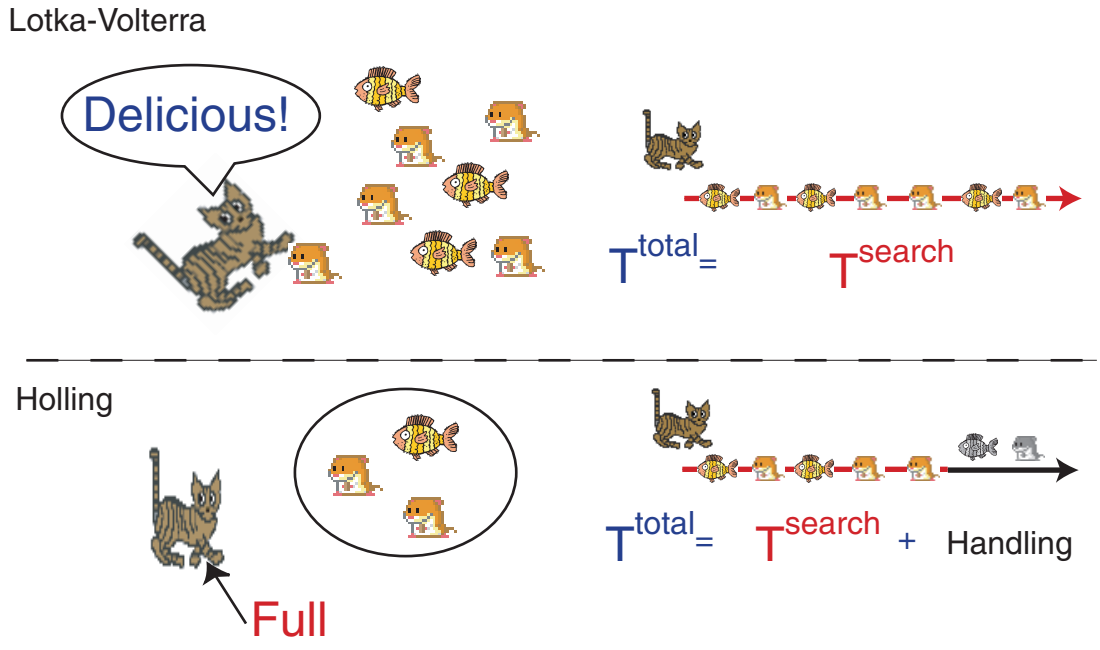


Figure 2.2: Lotka-Volterra and Holling type functional response.

In this sense, parameter h_{ij} is called the handling time. The function $g(N_j)$ is a monotonically increasing function but saturated to $1/h_{ij}$ for $N_j \to \infty$. If a predator does not need handling times $h_{ij} = 0$ (thus $T^{\text{total}} = T^{\text{search}}$), the Lotka-Volterra functional response (2.2) is obtained (Figure 2.2). We also notice that the equation (2.4) is based on the assumption that different prey species may be encountered and attacked by the predator at the same time within the (common) search time T^{search}.

The population dynamics (2.1) described in terms of energy flow can also be written in the form

$$\frac{dN_i(t)}{dt} = N_i(t)G_i, \tag{2.8}$$

where the time dependent coefficient G_i is called the growth rate of species i. According to which functional response is taken, we have two types of growth rates:
(Lotka-Volterra Type)

$$G_i = \sum_{j\in B_i} \lambda_{ij}\, a_{ij}N_j - \sum_{k\in R_i} a_{ki}N_k - \alpha_i - \beta_i N_i. \tag{2.9}$$

(Holling Type)

$$G_i = \sum_{j\in B_i} \frac{\lambda_{ij}a_{ij}N_j}{1+\sum_{j'\in B_i} h_{ij'}a_{ij'}N_{j'}} - \sum_{k\in R_i} \frac{a_{ki}N_k}{1+\sum_{i'\in B_k} h_{ki'}a_{ki'}N_{i'}} - \alpha_i - \beta_i N_i. \tag{2.10}$$

In contrast to equation (2.1), in equation (2.8), all the biologically interpretable terms are hidden into the function G_i. But this form is important for the derivation of the dynamics for adaptive behavior, therefore we also refer to the equation (2.8) from time to time in the following sections.

2.1.2 Adaptive foraging

According to behavioral ecology, (time dependent) behavior contributes to the survivorship, reproduction and therefore population growth of species, and in the study of food webs where the prey-predator relationships are the main focus, foraging is one of the most fundamental behavior. It is actually known that animals take different foraging options according to the relation between the "value" of prey and the environment surrounding them (Werner and Hall, 1974; Elner and Hughes, 1978). Therefore we first introduce adaptive foraging but also discuss the effect of predator avoidance behavior in the next subsection 2.1.3.

A classical method by Stephens and Krebs (1986) to incorporate the effect of foraging behavior into the model is the "all or none" rule that a prey should always or never be taken upon encounter, which leads to a functional response

$$g_{ij} = \frac{a_{ij}p_{ij}N_j}{1+\sum_{j'=1} h_{ij'}a_{ij'}p_{ij'}N_{j'}}. \tag{2.11}$$

The parameter p_{ij} is the probability that predator i attacks prey j on an encounter, and determined by the so called prey algorithm so that the energy flow to i is maximized and as a result takes only the value 0 or 1 (Charnov, 1976; Stephens and Krebs, 1986). This result is based on the assumptions that different resources can be substituted for each other, and that the adaptive behavior of predators does not affect encounter rates, but only the decision to attack a prey item when encountered.

Diet choice and patch choice

We will focus on the case where the encounter rates themselves are affected by the adaptive behavior. In the literature, there can be found two versions of Holling type II functional response with adaptive behavior. The first one is obtained by replacing T^{search} in the equation (2.4) by prey dependent search time T_j^{search} with the assumption that predators divide their searching time among the different prey species. This leads to the expression

$$g_{ij} = \frac{n_j}{T^{\text{total}}} = \frac{a_{ij} f_{ij} N_j}{1 + \sum_{j'=1} h_{ij'} a_{ij'} f_{ij'} N_{j'}}, \tag{2.12}$$

where $f_{ij} = T_j^{\text{search}} / \sum_{j' \in B_i} T_{j'}^{\text{search}}$ is the proportion of time devoted to prey j, which we call foraging "efforts" of i to j. This form of foraging model is used for instance in Brose et al. (2003) and Abrams and Matsuda (2004). Of course, the sum of all foraging efforts that a predator i invests in its prey species j is unity,

$$\sum_{j \in B_i} f_{ij} = 1. \tag{2.13}$$

This is a linear constraint on the efforts.

To make the things more clear, we discuss the assumption behind the model in more detail. In the original equation (2.4), the total searching time (or effort) T^{search} is used for all the prey in common. But in order to incorporate adaptive behavior into the model, it is assumed that predators distribute their available time (efforts) between different prey to get the amount of food $n_j = a_{ij} N_j T_j^{\text{search}} = a_{ij} N_j f_{ij} T^{\text{search}}$, where $\sum_{j \in B_i} T_j^{\text{search}} = T^{\text{search}}$. And, this also assumes implicitly that the searching effort for one prey T_j^{search} is used only to hunt prey j and never contributes to find other prey, i.e., species can only search for one type of prey at the same time, which is antipole of the original equation (2.4).

In reality a predator will feed not only on the target species j during a given time, but it can also simultaneously come across and feed on species that are similar to the target species. We propose an intermediate foraging model later in subsection 2.1.4, where it is allowed that a foraging effort for prey j contributes to find other prey j', leading to the amount of found food $n_j \geq a_{ij} N_j T_j^{\text{search}} = a_{ij} N_j f_{ij} T^{\text{search}}$ with $\sum_{j \in B_i} f_{ij} = 1$, whose effects can be embedded into nonlinearity of the constraints on the efforts.

The second version assumes that different prey live in different patches and therefore that a predator i invests the proportion f_{ij} of its total time T^{total} to stay

in patch j. In this case, predetor i stays in patch j for $T_j^{\text{total}} = T_j^{\text{search}} + h_{ij}n_j$ and gets prey item j of the amount $n_j = a_{ij}N_jT_j^{\text{search}}$. Therefore the functional response has the form

$$g_{ij} = \frac{n_j}{T^{total}} = f_{ij}\frac{a_{ij}N_j}{1 + h_{ij}a_{ij}N_j}, \tag{2.14}$$

with $f_{ij} = T_j^{\text{total}}/T^{\text{total}}$. This model is based on the assumption that the habitats are completly segregated, therefore T_j^{search} is only used to search for prey j. In contrast to this second version, in the first version, we can assume that prey live in a same habitat and are mixed in it. We refer to the first version simply as Holling functional response (or with "diet choice model") and the second version as Holling functional response patch choice model (Figure 2.3).

The difference between the two versions of adaptive foraging is irrelevant so long as we consider the Lotka-Volterra model, since both versions lead to the same equation. Lotka-Volterra functional response (2.2) then becomes (Matsuda and Namba, 1991; Kondoh, 2003)

$$g_{ij} = f_{ij}a_{ij}N_j\,. \tag{2.15}$$

We call from now on a variable (or function) multiplied by a foraging effort f_{ij} "effective variable" and the original variable "potential variable". For example, a_{ij} is a potential connection strength and $a'_{ij} = f_{ij}a_{ij}$ is an effective connection strength.

Adaptive foraging dynamics

Animals change their foraging behavior in response to the environment, in which they live, to improve the survivorship. And such change occurs evolutionarily (evolutionary process) or behaviorally (learning process). Within the framework of food webs, the environment of an animal consists of its predators and prey (i.e., other animals) whose states are also changing in time. Here the state is anything

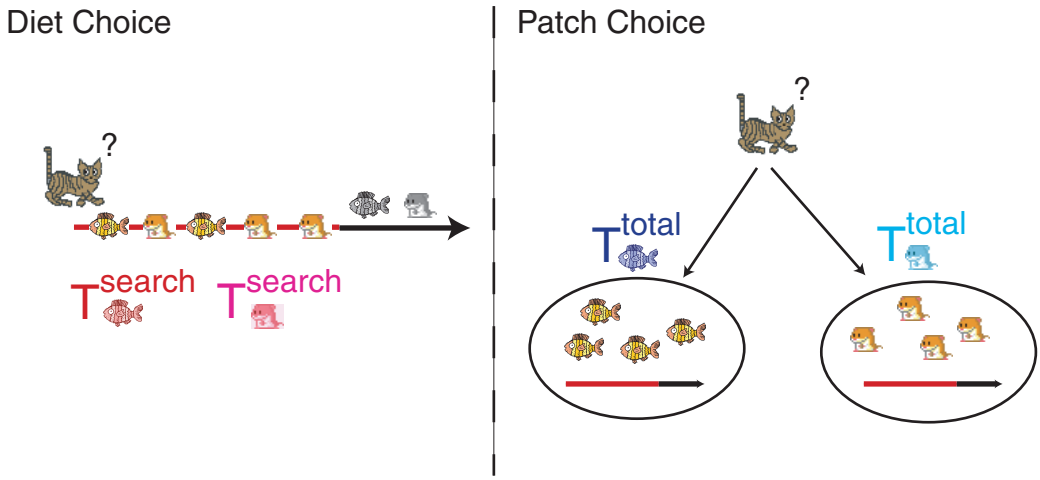


Figure 2.3: Diet choice and patch choice.

that affects the population growth (or survivorship) of the animal, for instance, the population sizes or foraging behavior.

This situation is exactly same as what has been studied in game theory (Osborne and Rubinstein, 1994; Weibull, 1996; Hofbauer and Sigmund, 1998), where agents are trying to maximize their return (pay-off) by choosing appropriate strategies but the return depends on the decision of other agents (more generally states of other agents, environment). In fact, for the Lotka-Volterra model, we can directly translate the jargons used here into the words of game theory as "species i" to "player i", "i feeds on prey $j \in B_j$" to "i chooses strategy j from the strategy set B_i" and "distribution of foraging efforts $\{f_{ij}\}$" to "mixed strategy $\{f_{ij}\}$". What species try to maximize by changing strategies f_{ij} is its growth rate G_i. Therefore the pay-off of pure strategy $j \in B_i$ of i is the potential energy in-flow $\lambda_{ij}a_{ij}N_j$ which i can control by tuning foraging efforts $\{f_{ij}\}$ in the growth rate G_i.

Then the adaptation process to the environment is described by replicator dynamics

$$\frac{df_{ij}(t)}{dt} = \kappa f_{ij}(t)(\lambda_{ij}a_{ij}N_j - \sum_{j' \in B_i} \lambda_{ij'}a_{ij'}f_{ij'}N_{j'}) \,, \tag{2.16}$$

where κ is the ratio between the time scales of adaptive foraging and of population dynamics. For the Holling functional response patch choice model (2.14), the pure strategy pay-off can be defined in a similar way. In this case, the pure strategy pay-off is given by $\lambda_{ij}a_{ij}N_j/(1 + h_{ij}a_{ij}N_j)$.

For Holling type II functional response (2.12), the definition of pure strategy pay-off in our context is difficult, because the mixed strategy $\{f_{ij}\}$ contributes to the growth rate in a nonlinear fashion contrary to game theory (and Lotka-Volterra model or Holling functional response patch choice model). But in literature the potential energy in-flow $\lambda_{ij}a_{ij}N_j$ or $\lambda_{ij}a_{ij}N_j/(1+h_{ij}a_{ij}N_j)$ is nevertheless adopted as the pure strategy pay-off, leading to the same equation (2.16), e.g., Kondoh (2006). In spite of the simplicity of this form and clarity of pure strategy pay-off, the biological meaning of the equation (2.16) is somewhat unclear.

If we return to the argument that animals are trying to maximize their growth rate by changing its behavior, another equation is derived:

$$\frac{df_{ij}(t)}{dt} = \kappa f_{ij}(t)(\partial G_i/\partial f_{ij} - \langle \partial G_i/\partial f_{ij} \rangle) \,, \tag{2.17}$$

where $\langle \partial G_i/\partial f_{ij} \rangle = \sum_{j \in B_i} f_{ij}\partial G_i/\partial f_{ij}$ is the mean change in the growth rate due to a change of the efforts. For the Lotka-Volterra model, this equation leads to (2.16). In this equation, the efforts are changed such that the growth rate increases and the constraint (2.13) is preserved. Therefore this equation solves the maximization problem of growth rate G_i as a function of efforts $\{f_{ij}\}$ under the linear constraint (2.13).

At a fixed point, the efforts into prey species i for which the inequality

$$\partial G_i/\partial f_{ij}|_{f_{ij}=0} < \langle \partial G_i/\partial f_{ij} \rangle \tag{2.18}$$

holds, vanish and vice versa. For the Lotka-Volterra systems, the meaning of this is clear. In this case $\partial G_i/\partial f_{ij} = \lambda_{ij}a_{ij}N_j$ is the potential energy in-flow from j,

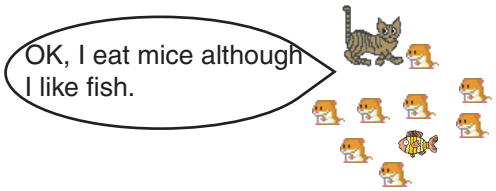


Figure 2.4: The cat does not search for fish because the population size of fish is small and the energy intake from fish is expected to be small.

and individuals of species i eventually stop searching for prey j (i.e., $f_{ij} \to 0$) if the energy in-flow from j is smaller than other species' ones, and they concentrate only on searching the most valuable prey (Figure 2.4). For convenience, we refer to the term $\partial G_i/\partial f_{ij}$ as potential pay-off because this term determines the "value" of prey j from the i's view point, even though this does not correspond to the original meaning of pay-off.

If there was no population dynamics (i.e., the environment was fixed), a predator would according to these rules put all its effort into the most profitable prey, and all other efforts would become zero. Of course, this does not remain so under population dynamics. If a predator feeds only on its most profitable prey, the population size of this prey decreases in general, until it becomes equally profitable to feed on a different prey. The combined population dynamics and adaptive dynamics lead therefore to fixed points where efforts can be different from unity or zero (Matsuda et al., 1994; Matsuda et al., 1996).

2.1.3 Predator avoidance

Foraging behavior is vital from the predators' eye view. They control their foraging strategy to improve the efficiency of their reproduction. On the other hand, from the view point of prey, avoiding dangerous predators is a main activity, even though there is a difference between foraging and predator avoidance: Forging is a necessary activity for animals to survive while predator avoidance not. In this subsection we discuss the effect of predator avoidance coupled with foraging behavior.

Lotka-Volterra model with linear constraints

The usual way of modeling predator avoidance consists in assigning efforts to the avoidance behavior (Matsuda et al., 1994; Matsuda et al., 1996; Strauss et al., 2002; Lass and Spaak, 2003; Strauss et al., 2004). Each species tries to maximize its growth rate by devoting some effort to reducing the probability of being caught by predators. The growth rate of population i is now

$$G_i = \sum_{j \in B_i} \lambda_{ij} f_{ij} a_{ij} (1 - v_{ji}) N_j - \sum_{k \in R_i} (1 - v_{ik}) a_{ki} f_{ki} N_k - \alpha_i - \beta_i N_i, \qquad (2.19)$$

where v_{ik} represents the fraction of time that species i spends avoiding predator k. The potential pay-off of the strategy f_{ij} is given by $\lambda_{ij} a_{ij} (1 - v_{ji}) N_j$ which now depends also on the predator avoidance effort v_{ji} of prey j against i, and $a_{ki} f_{ki} N_k$ is the potential pay-off obtained by concentrating on the effort v_{ik}.

So $f_{ij} \geq 0$ and $v_{ik} \geq 0$ must be constrained by

$$\sum_{j \in B_i} f_{ij} + \sum_{k \in R_i} v_{ik} = 1 \,, \tag{2.20}$$

implying that total available time for searching and avoiding is exactly divided into $(\cdots, f_{ij}, \cdots, v_{ik}, \cdots)$ and all the efforts are completely independent or exclusive between each other. Then the equation describing the dynamics for the behavior is, instead of equation (2.17) for the efforts,

$$\begin{aligned} \frac{df_{ij}(t)}{dt} &= \kappa f_{ij}(t)(\partial G_i/\partial f_{ij} - \langle \partial G_i/\partial x \rangle) \\ \frac{dv_{ik}(t)}{dt} &= \kappa v_{ik}(t)(\partial G_i/\partial v_{ik} - \langle \partial G_i/\partial x \rangle) \,, \end{aligned} \tag{2.21}$$

with

$$\langle \partial G_i/\partial x \rangle = \sum_{j \in B_i} f_{ij} \partial G_i/\partial f_{ij} + \sum_{k \in R_i} v_{ij} \partial G_i/\partial v_{ik} \,.$$

Now we investigate shortly the fixed point condition of (2.21). As is mentioned in the last subsection, the potential pay-offs with zero efforts must be smaller than the average pay-off $\langle \partial G_i/\partial x \rangle$ and vice versa, which at the same time means that all the pay-offs with nonzero efforts must be same at a fixed point (or we can find this immediately from the equation):

$$\partial G_i/\partial f_{ij} = \partial G_i/\partial f_{ij'} = \partial G_i/\partial v_{ik} = \partial G_i/\partial v_{ik'} = \langle \partial G_i/\partial x \rangle := \Gamma_i, \tag{2.22}$$

for nonzero efforts $f_{ij}, f_{ij'}, v_{ik}, v_{ik'}$. Because the growth rate G_i is linear in f_{ij} and v_{ik}, the coefficients of the variables f_{ij} and v_{ik} can be replaced by Γ_i. Now let $B_i^{(1)}$ ($R_i^{(1)}$) be the set of prey (predators) that are hunted (avoided) by species i, and $B_i^{(2)}$ ($R_i^{(2)}$) be the set of species for which the efforts are zero. Then the growth rate at the fixed point is evaluated as

$$\begin{aligned} G_i &= \sum_{j \in B_i^{(1)}} f_{ij}\Gamma_i - \sum_{k \in R_i^{(1)}} (1 - v_{jk})\Gamma_i - \sum_{m \in R_i^{(2)}} f_{mi} a_{mi} N_m - \alpha_i - \beta_i N_i \\ &= \Big(\sum_{j \in B_i^{(1)}} f_{ij} + \sum_{k \in R_i^{(1)}} v_{jk} \Big)\Gamma_i - \sum_{k \in R_i^{(1)}} \Gamma_i - \sum_{m \in R_i^{(2)}} f_{mi} a_{mi} N_m - \alpha_i - \beta_i N_i \\ &= (1 - R_i^{(1)})\Gamma_i - \sum_{m \in R_i^{(2)}} f_{mi} a_{mi} N_m - \alpha_i - \beta_i N_i, \end{aligned} \tag{2.23}$$

where $R_i^{(1)}$ in the last expression is the total number (not the set) of predators avoided by species i.

It follows that the growth rate G_i is always negative, unless no predators are avoided (i.e., $R_i^{(1)} = 0$). Consequently, in computer simulations the avoidance variables always go to zero or the species becomes extinct (Figure 2.5). This means that devoting to foraging activity is always more beneficial than predator avoidance

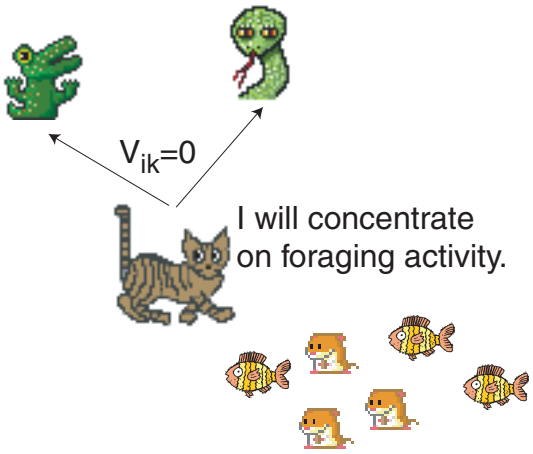


Figure 2.5: Foraging and predator avoidance.

activity, thus this simple implementation of predator avoidance does not work. This is also true for non specific defense, where an effort for predator avoidance v is effective for all the predators. In this case, the constraint is $\sum_{j\in B_i} f_{ij} + v = 1$ and the growth rate is

$$\begin{aligned} G_i &= \sum_{j\in B_i^{(1)}} f_{ij}\Gamma_i - \sum_{k\in R_i^{(1)}} (1-v)\Gamma_i - \sum_{m\in R_i^{(2)}} f_{mi}a_{mi}N_m - \alpha_i - \beta_i N_i \\ &= (1-R_i^{(1)})(1-v)\Gamma_i - \sum_{m\in R_i^{(2)}} f_{mi}a_{mi}N_m - \alpha_i - \beta_i N_i \le 0. \end{aligned} \tag{2.24}$$

If, however, we assume that foraging contributes to the growth rate in a nonlinear way,

$$G_i = A\Big(\sum_{j\in B_i} \lambda_{ij} f_{ij} a_{ij}(1-v_{ji})N_j\Big) - \sum_{k\in R_i} (1-v_{ik})a_{ki}f_{ki}N_k - \alpha_i - \beta_i N_i \tag{2.25}$$

with $A(x) > x$, then we can obtain nonzero values of v_{ik} at a fixed point. This can be for instance found in Matsuda et al. (1994), where the function $A(x) \propto \sqrt{x}$ for $x < 1$ is used.

Holling model with predator avoidance

For the Holling functional response patch choice model, we obtain the same conclusion because of the linear dependence of the growth rate on the efforts. However the analytical investigation for the Holling functional response diet choice model becomes very complicated. Therefore we did not perform a thorough analysis of the Holling model with predator avoidance. However, it appears from computer simulations that in the case of linear constraints the avoidance coefficients decrease to zero, while they can remain nonzero for nonlinear constraints.

As we have seen, linear constraints on the efforts do not allow for any predator avoidance behavior if the type of population dynamics discussed here is used. This means that it is even more evident that linear constraints on the efforts might

not be realistic. They (i.e., linear constraints) imply that a prey cannot feed at all while hiding from the predator. In contrast, empirical research suggests that predator avoidance behavior reduces only partially the capability of consuming food by forcing prey species to feed less or to exploit less profitable resources (Loose and Dawidowicz, 1994; Peckarsky, 1996; Turner et al., 2000; Amarasekare, 2006). This leads us to considering nonlinear constraints.

2.1.4 Nonlinear constraints on efforts

If the prey of a predator occur in different sub-habitats, adaptive foraging implies that the predator will focus its searching activities on the sub-habitat with the more profitable prey (Murdoch et al., 1975). In this case, searching for specific prey species is mutually exclusive and switching to a specific prey implies that the encounter rates are reduced for all other prey. In contrast, in spatially homogeneous habitats adaptive foraging does not change the encounter rates between a predator and its various prey (Siddon and Witman, 2004). Nevertheless, predators tend to focus on their more profitable prey. In both situations, there are several reasons rendering it unlikely that a predator puts all its effort exclusively into the most profitable prey as suggested by the linear constraint (2.13). First, few habitat subdivisions are strict and even in structured habitats predators still encounter alternative prey while searching for specific prey (Murdoch et al., 1975). Efforts into different activities are therefore not completely mutually exclusive. Second, predators may not be capable to confine their search completely to the most profitable prey. This would possibly prevent them from noticing increasing abundances of different prey. Third, a broader variety of food might be important in order to obtain all needed nutrients, and therefore it might be better to adjust foraging behavior only to some extent to food abundances. Indeed, empirical data suggest that a predator does not put all its effort in its most profitable prey (Murdoch et al., 1975; Siddon and Witman, 2004), but that the ratio of the rates of consumption of two prey (j, j') is given by

$$\frac{a_{ij} f_{ij} N_j}{a_{ij'} f_{ij'} N_{j'}} \propto \left(\frac{a_{ij} N_j}{a_{ij'} N_{j'}} \right)^b \tag{2.26}$$

with an exponent b that is larger than 1 if adaptive foraging takes place (Greenwood, 1979; Elliott, 2004).

Such a law is obtained if we impose nonlinear constraints on the efforts,

$$\sum_{j \in B_i} {f_{ij}}^r = 1 \,. \tag{2.27}$$

Maximizing the consumption rate

$$a_{ij} f_{ij} N_j + a_{ij'} f_{ij'} N_{j'}$$

with respect to the efforts then leads to equation (2.26) with $b = r/(r-1)$.

In the limit $r = 1$, we obtain again linear constraints. We would then have $b \to \infty$, implying that the predator focuses completely on the most profitable (or

valuable) prey. In the opposite limit $r \to \infty$, there is no adaptive foraging, and $b \to 1$. In this sense, this is an intermediate model, and by choosing an appropriate value of r, one can adjust the extent of adaptive foraging.

Nonlinear constraints on the efforts in Holling functional response (2.12) and (2.14) also lead to a relation similar to (2.26), which is important as a Type II functional response is considered more realistic. More precisely, we obtain exactly (2.26) if we start from (2.14) with nonlinear constraints on the efforts. If we start from (2.12), we get $\frac{F_j}{F_{j'}} = \left(\frac{A_j}{A_{j'}}\right)^{r/(r-1)} \left(\frac{1+(h_{j'}-h_j)F_{j'}}{1+(h_j-h_{j'})F_j}\right)^{1/(r-1)}$, where $F_j = a_{ij} f_{ij} N_j$, $A_j = a_{ij} N_j$. If the handling times are not too different from each other, this can be well approximated by (2.26).

Generic derivation of the constraints

In this subsection, we motivate in more detail nonlinear constraints on the foraging efforts and derive the time evolution for the efforts. The assumption is that a predator searching for one prey may at the same time encounter another prey that requires a similar search strategy (Figure 2.6).

Let us now denote the proportion of time predator i searches for prey j with $f_{ij} = T_j^{\text{search}}/T^{\text{search}}$. The sum $\sum_{j \in B_i} f_{ij} = 1$ is normalized as before, however, we now assume that predator i may also encounter prey j' while searching for prey j. We denote with $\rho_{jj'}^{(i)}$ the similarity of prey j and prey j' for predator i. Then the encounter rate of predator i with prey j becomes

$$a_{ij} \tilde{f}_{ij} = a_{ij} \sum_{j' \in B_i} f_{ij'} \rho_{ij'}^{(i)} ,$$

where we now have to find the constraint on the effective efforts $\tilde{f}_{ij}$. Because the similarity takes a positive value this means that $a_{ij} \tilde{f}_{ij} \geq a_{ij} f_{ij}$. A detailed model that specifies the similarity between every pair of species would yield expressions for the $\{\tilde{f}_{ij}\}$, however, we try to find here a generic way of arriving at constraints

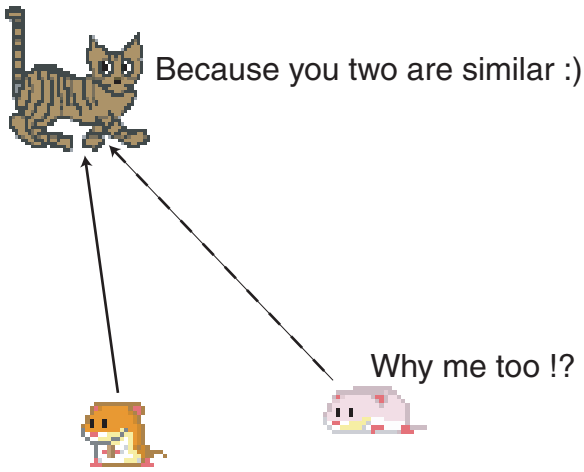


Figure 2.6: Accidental encounter and feeding.

for the effective efforts. The average size of an effective effort is given by

$$\begin{aligned} \left\langle \tilde{f}_{ij} \right\rangle &= \left\langle \sum_{j' \in B_i} f_{ij'} \rho^{(i)}_{jj'} \right\rangle \\ &\simeq \sum_{j' \in B_i} f_{ij'} \left\langle \rho^{(i)}_{jj'} \right\rangle = \left\langle \rho^{(i)}_{jj'} \right\rangle . \end{aligned} \tag{2.28}$$

The step from the first to the second line of this calculation is to be understood as a rough estimate of the order of magnitude of $\left\langle \tilde{f}_{ij} \right\rangle$ rather than an exact calculation. Next, we have to estimate the average size $\left\langle \rho^{(i)}_{jj'} \right\rangle$ of the overlap between two prey species for predator i. We can expect the overlap between a randomly chosen pair of prey species to be smaller when a predator has more prey and therefore set

$$\left\langle \rho^{(i)}_{jj'} \right\rangle \propto B_i^{-y}$$

with B_i denoting the number (not the set) of prey of species i, and y is an exponent between 0 and 1. The value of y cannot be larger than 1, since the overlap of prey j with itself must be 1, and therefore $\left\langle \rho^{(i)}_{jj'} \right\rangle \geq 1/B_i$. We then obtain

$$\begin{aligned} \sum_{j \in B_i} \left\langle \tilde{f}_{ij} \right\rangle &\simeq B_i \left\langle \tilde{f}_{ij} \right\rangle \\ &\simeq B_i \left\langle \rho^{(i)}_{jj'} \right\rangle \propto B_i B_i^{-y} \\ &= B_i^{1-y} \end{aligned}$$

or, by defining $r = 1/(1-y)$,

$$\sum_{j \in B_i} \left\langle \tilde{f}_{ij} \right\rangle^r \propto 1 .$$

We therefore introduce the constraint (2.27)

$$\sum_{j \in B_i} \tilde{f}_{ij}^{\,r} = 1$$

for the effective efforts. The value of the constant on the right-hand side could be different from 1, however, this can be taken into account by renormalizing other parameters, for instance the couplings a_{ij}. Because of $0 \leq y < 1$, we have $r \geq 1$. The special case $r = 1$ corresponds to the traditional linear constraints. From now on, we drop the superscript tilde for the effective efforts, even when we consider nonlinear constraints.

The condition that the growth rate is maximized subject to (2.27) can be implemented using the method of Lagrange multipliers. Defining $H_i = G_i - \gamma_i(\sum_{j \in B_i} f_{ij}^{\,r} - 1)$ with Lagrange-multipliers γ_i, we have

$$\begin{aligned} \frac{\partial H_i}{\partial f_{ij}} &= \frac{\partial G_i}{\partial f_{ij}} - r\gamma_i f_{ij}^{\,r-1} = 0 ; \\ \frac{\partial G_i}{\partial f_{ij}} &= r\gamma_i f_{ij}^{\,r-1} . \end{aligned} \tag{2.29}$$

Therefore

$$f_{ij}{}^{1-r}\frac{\partial G_i}{\partial f_{ij}} = f_{ij'}{}^{1-r}\frac{\partial G_i}{\partial f_{ij'}} = r\gamma_i, \tag{2.30}$$

for nonzero efforts f_{ij} and $f_{ij'}$. On the other hand,

$$\begin{aligned} r\gamma_i &= f_{ij}{}^{1-r}\frac{\partial G_i}{\partial f_{ij}}\,; \\ \sum_{j\in B_i} f_{ij}{}^{r} r\gamma_i &= \sum_{j\in B_i} f_{ij}\frac{\partial G_i}{\partial f_{ij}} = r\gamma_i\,. \end{aligned} \tag{2.31}$$

Thus the solution of the maximization problem must satisfy the condition

$$f_{ij}{}^{1-r}\frac{\partial G_i}{\partial f_{ij}} = \sum_{j\in B_i} f_{ij}\frac{\partial G_i}{\partial f_{ij}}. \tag{2.32}$$

Then the dynamics of the efforts (2.17) is modified with nonlinear constraints

$$\frac{df_{ij}(t)}{dt} = \kappa f_{ij}(t)\left(f_{ij}{}^{1-r}\partial G_i/\partial f_{ij} - \langle \partial G_i/\partial f_{ij}\rangle\right)\,, \tag{2.33}$$

with $\langle \partial G_i/\partial f_{ij}\rangle = \sum_{j\in B_i} f_{ij}\partial G_i/\partial f_{ij}$. The fixed point of this dynamics gives the solution (2.32) of the maximization problem. Moreover this equation preserves the constraint with nonlinearity r:

$$\begin{aligned} \sum_{j\in B_i}\frac{df_{ij}{}^{r}}{dt} &= \sum_{j\in B_i} r f_{ij}{}^{r-1}\frac{df_{ij}}{dt} && (2.34)\\ &= r\kappa\sum_{j\in B_i} f_{ij}{}^{r-1} f_{ij}\left(f_{ij}{}^{1-r}\partial G_i/\partial f_{ij} - \langle \partial G_i/\partial f_{ij}\rangle\right) && (2.35)\\ &= r\kappa\sum_{j\in B_i} f_{ij}\partial G_i/\partial f_{ij} - r\kappa\sum_{j\in B_i} f_{ij}{}^{r}\langle \partial G_i/\partial f_{ij}\rangle && (2.36)\\ &= 0. && (2.37) \end{aligned}$$

For Lotka-Volterra dynamics, at a fixed point, we can easily eliminate the efforts from the expression for γ_i by making use of the constraint (2.27), and we obtain an explicit expression for efforts:

$$r\gamma_i = \left[\sum_{j\in B_i}\left(\frac{\partial G_i}{\partial f_{ij}}\right)^{r/(r-1)}\right]^{1-1/r}\,, \tag{2.38}$$

thus

$$f_{ij}{}^{1-r}\frac{\partial G_i}{\partial f_{ij}} = \left[\sum_{j\in B_i}\left(\frac{\partial G_i}{\partial f_{ij}}\right)^{r/(r-1)}\right]^{1-1/r}\,. \tag{2.39}$$

Since $\partial G_i/\partial f_{ij}$ does not include efforts, this equation gives the solution with nonlinear constraints $r > 2$.

Let us from now on consider the case $r = 2$ with Lotka-Volterra dynamics. We now have the constraint

$$\sum_{j \in B_i} {f_{ij}}^2 = 1, \tag{2.40}$$

or in vector notation

$$|\vec{f_i}| = 1, \tag{2.41}$$

where $\vec{f_i}$ is a vector constructed by the efforts of i to $j \in B_i$: $(\cdots, f_{ij}, \cdots)$. We can rewrite growth rate and the population dynamics also in a vector form,

$$G_i = \vec{f_i} \cdot \vec{g_i} - \sum_{k \in R_i} a_{ki}\, f_{ki} N_k - \alpha_i - \beta_i N_i, \tag{2.42}$$

where $\vec{g_j}$ is the potential pay-off vector defined by $(\cdots, \lambda_{ij}\, a_{ij} N_j, \cdots)$. The first term satisfies the inequality

$$\vec{f_i} \cdot \vec{g_i} \leq |\vec{f_i}||\vec{g_i}| = |\vec{g_i}|\,, \tag{2.43}$$

and the equality holds only if

$$\vec{f_i} = \vec{g_i}/|\vec{g_i}| \tag{2.44}$$

or

$$f_{ij} = \lambda_{ij} a_{ij} N_j / |\vec{g_i}|. \tag{2.45}$$

If this is achieved, the growth rate (2.42) is maximized. That is, the effort of i to j is exactly proportional to the potential pay-off prey j offers and thus proportional to time dependent variable N_j. Therefore $f_{ij} \to 0$ for $N_j \to 0$ except for the case where the total potential pay-off also goes to zero: $|\vec{g_i}| \to 0$. That is, the effort into a prey with vanishing population size vanishes (if other prey is present). And this happens for all the species (f_{ki}), therefore

$$G_i \to |\vec{g_i}| - \alpha_i \tag{2.46}$$

for $N_i \to 0$. And if in this situation the total pay-off $|\vec{g_i}|$ is large enough to compensate mortarity α_i, the population size N_i again becomes larger according to the population dynamics $dN_i/dt = G_i N_i$.

Predator avoidance with nonlinear constraints

Nonlinear constraints on foraging efforts and predator avoidance mean that even while hiding from predators, the species can act on foraging activity and vice versa. If we take nonlinear constraints with $r = 2$

$$\sum_{j \in B_i} {f_{ij}}^2 + \sum_{k \in R_i} {v_{ik}}^2 = 1, \tag{2.47}$$

then exactly as in the model without predator avoidance behavior, the vector

$$(\cdots, \partial G_i/\partial f_{ij}, \cdots, \partial G_i/\partial v_{ik}, \cdots) \tag{2.48}$$

must be parallel to the unit vector

$$(\cdots, f_{ij}, \cdots, v_{ik}, \cdots). \tag{2.49}$$

when the growth rate G_i is maximized. This means that each f_{ij} is proportional to N_j and each v_{ik} is proportional to N_k, and we obtain nonzero values for the v_{ik} at a fixed point, that it, contrary to linear constraints, species show predator avoidance behavior. This analytical result is confirmed in computer simulations.

Since there are so many reasons to allow for nonlinear constraints on the efforts, we will study below model networks with nonlinear constraints as well as with linear constraints. Whether linear or nonlinear constraints are more appropriate, should depend on the extent to which species in the food web are aggregated. The higher the level of aggregation, the more do "species" differ from each other, because similar species are grouped together. It is thus easier for predators to discriminate between prey, and the strategies required for searching for different prey are more distinct. One might expect that for higher levels of aggregation the exponent r should be closer to 1.

2.1.5 Interspecific competition

In addition to being affected by energy flow due to prey-predator interactions, population dynamics can be influenced by competition between different species, which is not described by the energy flow in a web. Connel (1983) reported that competition had been found in 55 % of 215 surveyed species by reviewing 72 experimental studies on competition in literature and, in parallel, Shoener (1983) reviewed 150 field experiments and found competition in 75 % of the species studied.

According to Shoener (1983, 1985), the mechanisms of interspecific competition can be classified into 6 categories: 1. Consumptive (using limiting prey), 2. Preemptive (using limiting space), 3. Overgrowth (one species growing over another and blocking light), 4. Chemical (producing toxins), 5. Territorial (fighting other behavior in defense of territory) and 6. Encounter (transient interactions directly over specific resources). Consumptive competition is the most common form of competition (occurring in 37.8 % of the investigated cases), and the encounter competition is the second most (14.1 %). The first three forms of competition occur indirectly through a common limiting resource and are called exploitative competition and the last three forms occur directly and are called interference competition.

The consumptive competition is already included in the population dynamics (2.1), because, for a predator i, presence of another predator i' that feeds on a same prey, which reduces the population size of the prey, negatively affects the population dynamics of i and vice versa. We present here how other forms of competition are included into the model.

Niche overlap

Often interspecific competition is modeled by the similarity of niches (or niche overlap). Niche is defined as the place of a species in an ecosystem and specified by all the components of the environment which the species interacts with (Grinnell, 1917). To model competition between species, Hutchinson (1957) suggested to represent a niche by a point $\vec{p}$ in a multidimensional space whose axes correspond to resource utilizations (i.e., p_j is the utilization of resource j), and Pianka (1973) proposed to measure the niche overlap by

$$O_{ii'} = O_{i'i} = \frac{\sum_j p_{ij} p_{i'j}}{\sqrt{\sum_j p_{ij}^2}\sqrt{\sum_j p_{i'j}^2}}, \tag{2.50}$$

where the sum $\sum_j$ is taken over all the species (If i does not utilize j, $p_{ij} = 0$).

In the study of model food webs, this form of index can be found for example in Bastolla et al., (2002). They defined the niche overlap in terms of potential connection strength

$$p_{ij} = a_{ij}, \tag{2.51}$$

where $a_{ij} = 0$ for $j \notin B_i$ and incorporated the index (2.50) as a competition into their model by adding the competition terms on the right-hand side of (2.1):

$$\frac{dN_i(t)}{dt} = \sum_{j\in B_i} \lambda_{ij} g_{ij}(t) N_i(t) - \sum_{k\in R_i} g_{ki}(t) N_k(t) - \alpha_i N_i(t) - \sum_{i'\in C_i} c_{ii'} N_i(t) N_{i'}(t), \tag{2.52}$$

where C_i is the set of species (including i) that shear at least one prey with i. For $i = i'$, c_{ii} denotes the intraspecific competition and takes the value β_i and for $i \neq i'$, $c_{ii'} = \sigma\beta_i O_{ii'}$, where $\sigma \leq 1$ represents the strength of interspecific competition compared to intraspecific competition.

If we incorporate competitions of the form (2.51) into the model with adaptive behavior, the adaptive dynamics (2.17) or (2.33) is not affected because the potential pay-off $\partial G_i/\partial f_{ij}$ does not include the competition terms.

Niche differentiation

In the model with adaptive foraging, we can define the niche of a species based on the effective connection strengths:

$$p_{ij} = f_{ij} a_{ij}. \tag{2.53}$$

In this case, the competition terms are affected by the foraging dynamics. Recalling that a species tries to maximize its growth rate by controlling foraging behavior and that the competition terms negatively affect the growth rate, we see that each species changes its niche so that the niche overlap is avoided and the competition

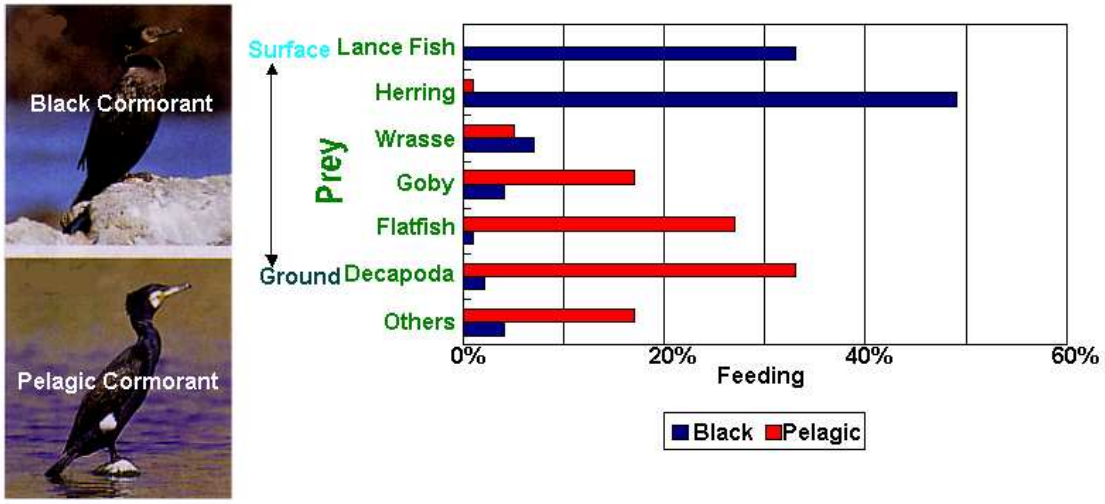


Figure 2.7: An example of niche segregation by two similar species Black Cormorant and Pelagic Cormorant (Ishikawa et al., 2004). They feed on different prey and the competition is reduced.

becomes small. This phenomenon is known as niche differentiation or niche segregation, and is observed in natural systems (Bovbjerg, 1970; Inoue, 1978; Pacala and Roughgarden, 1982; see Figure 2.7).

It should be noted that consumptive competition is also reduced by foraging dynamics, because the population size of a prey is in general small if many predators feed on it and therefore some predators tend to stop feeding on the prey. As a result the consumptive competition will be reduced.

Beddington functional response

There is a model where competition is included in the functional response. We assume that an individual of a species spends time on interrupting or fighting other species. Then the total time (2.6) is modified to

$$T^{\text{total}} = T^{\text{search}} + \sum_{j \in B_i} h_{ij} n_j + \sum_{i' \in C_i} T_{i'}^{\text{comp}}, \tag{2.54}$$

where $T_{i'}^{\text{comp}}$ is the time needed to fight species i'. The competition time $T_{i'}^{\text{comp}}$ is proportional to the population size of i' and search time T^{search}: $T_{i'}^{\text{comp}} = c_{ii'} N_{i'} T^{\text{search}}$, where the coefficient $c_{ii'}$ is larger when species i and i' are more similar. Then we obtain the functional response

$$g_{ij} = \frac{n_j}{T^{\text{total}}} = \frac{a_{ij} N_j}{1 + \sum_{j' \in B_i} h_{ij'} a_{ij'} N_{j'} + \sum_{i' \in C_i} c_{ii'} N_{i'}}, \tag{2.55}$$

called (generalized) Beddington functional response (Arditi and Michalski, 1996). Contrary to model (2.52), it is not assumed in this model that an individual is killed through competition, but it is just assumed that the effectiveness of hunting

reduces due to the competition time $T_{i'}^{\text{comp}}$. This form of functional response is used only once in chapter 5 in this dissertation.

2.2 Food web stability and food web structure

Let us now explore the consequences of using one or the other type of population dynamics or adaptive dynamics on the structure and stability of networks. We will first investigate the stability of small populations and find that adaptive foraging has always a stabilizing effect. Then, we will derive constraints on the number of links in the food web for the different types of models.

2.2.1 Stability of small populations due to adaptive foraging

First, we show that adaptive foraging has a stabilizing effect on food webs because it protects species with small population sizes. With linear constraints on the efforts, we obtained the result that the effort into all prey j for which the inequality (2.18) holds vanishes. For Lotka-Volterra dynamics, we have $\partial G_i/\partial f_{ij} = \lambda_{ij} a_{ij} N_j$, and therefore the effort into a prey vanishes when its population size becomes very small (as long as other prey with larger population sizes are present). This means that species in a food web have a higher chance of survival in the presence of adaptive dynamics. If the population of a species becomes very small, its population dynamics equation (2.9) reduces to

$$G_i \simeq \sum_{j \in B_i} \lambda_{ij}\, a_{ij}\, f_{ij} N_j - \alpha_i \,, \tag{2.56}$$

which means that a species can survive if only there is enough food for it to compensate for the death rate α. We have got a similar argument with $r = 2$ in the last section. This conclusion breaks down if species i is the only prey of one of its predators, or if all other prey of one of its predators have also a small population size.

Of course, small populations are at a high extinction risk, since accidents, genetics, or demography, may also kill them (MacArthur and Wilson, 1967; Soule and Simberloff, 1986; Wilcox, 1986; Raup, 1991), an effect of which is contained in our deterministic modeling only through a fixed extinction threshold. Even though we neglect stochastic effects, we expect that the main conclusion remains valid that the risk of extinction of a small population is smaller if there is adaptive foraging.

That predators can indeed drive their prey extinct has been documented for instance in biological control experiments (Simberloff and Stiling, 1996). Some of the predators that were introduced to control a pest have become important predators of other native species and eventually caused their extinction. A prominent example is given by the introduction of the Indian mongoose (Herpestes auropunctatus) to Hawaii and the islands of the West Indies that drove some native reptiles extinct (Lever, 1985).

In the same way as we did for Lotka-Volterra dynamics, we can also show for Holling type II dynamics that adaptive foraging of its predators allows a species to survive if only enough food is available for it, irrespective of the number and strength of predators, provided that the predators have other prey with larger population size. We have from equations (2.14) and (2.12) again

$$\frac{\partial G_i}{\partial f_{ij}} \propto N_j \,,$$

and therefore the effort into prey species vanishes the population size of which is so small that

$$\frac{\partial G_i}{\partial f_{ij}} < \left\langle \frac{\partial G_i}{\partial f_{ij}} \right\rangle \,.$$

We can therefore approximate the growth rates with functional responses (2.14) and (2.12) for small population sizes by

$$G_i \simeq \sum_{j \in B_i} f_{ij} \frac{\lambda_{ij} a_{ij} N_j}{1 + h_{ij} a_{ij} N_j} - \alpha_i$$

and

$$G_i \simeq \sum_{j \in B_i} \frac{\lambda_{ij} a_{ij} f_{ij} N_j}{1 + \sum_{j' \in B_i} h_{ij'} a_{ij'} f_{ij'} N_{j'}} - \alpha_i \,.$$

If only there is enough food available for the species to compensate for the death rate, a species can exist.

Now, let us consider the situation of nonlinear constraints on the efforts. According to (2.33), when $r > 1$ an effort always increases if it becomes too small. This means that at a fixed point all efforts are nonzero! This is no surprise if we remember that we have assumed that a predator can still pursue other activities while searching for a specific prey. Nevertheless, the effort into a prey with a small population size becomes very small, as we can immediately conclude from equation (2.29), where the left-hand side is proportional to N_j when N_j is very small for Lotka-Volterra dynamics as well as for Holling type II dynamics. The effort f_{ij} therefore also becomes very small unless species j is the only prey of species i or all prey of species i have a very small population size, in which case γ_i becomes very small. We can therefore repeat the reasoning that we did for the case of linear constraints to obtain the result that a very small population size always increases if only there is enough food for the species to compensate for the death rate α_i, irrespective of the number and population size of predators, provided that adaptive dynamics of the predators is fast enough and the species is not the only prey of a predator.

2.2.2 Link structure of Lotka-Volterra models

We first consider the Lotka-Volterra functional response $g_{ij} = a_{ij} f_{ij} N_j$ with the linear constraint and focus on fixed points of the combined adaptive foraging (2.17) and population dynamics (2.1).

In Matsuda and Namba (1991), Matsuda et al. (1994, 1996) , it was found that for Lotka-Volterra systems with several trophic levels the resulting webs must be so sparse that the number of links with nonzero effort is smaller than twice the number of existing species. This is due to the linear dependence of the functional G_i on the prey population sizes and the efforts. We will see that this constraint cannot be derived for nonlinear functional response of Holling type II, which indicates that the property is dependent of the functional response.

To avoid complications, we first assume a layered structure for the food web, i.e., the food web is perfectly divided into trophic levels and species in level l can feed only on species in level $l-1$. Therefore there is no omnivore. Then we generalize the calculation to include omnivores.

We denote the trophic level by a superscript. The fixed point of the adaptive dynamics (2.17) is given by

$$\begin{aligned} \partial G_i^{(l)}/\partial f_{ij} &= \partial G_i^{(l)}/\partial f_{ij'},\ (f_{ij}\neq 0, f_{ij'}\neq 0) && (2.57)\\ \lambda_{ij}\, a_{ij} N_j^{(l-1)} &= \lambda_{ij'}\, a_{ij'} N_{j'}^{(l-1)} =: \bar{g}_i. && (2.58) \end{aligned}$$

Now we denote by $C_i^{(l)}$ the number of prey species that species i in level l actually feeds on, that is, the number of variables f_{ij} that do not vanish. Then we see from equation (2.57) that there are $C_i^{(l)}$ homogeneous linear equations for the free variables $N_j^{(l-1)}$. This relation must hold for all i. Therefore, in order that the system of equations has a non-trivial solution, the following condition must hold:

$$\begin{aligned} \sum_{i=1}^{S^{(l)}} (C_i^{(l)}-1) &\equiv C^{(l)} - S^{(l)} < S^{(l-1)},\\ C^{(l)} &< S^{(l-1)} + S^{(l)}, \end{aligned} \qquad (2.59)$$

where $S^{(l)}$ is the number of species in level l and $C^{(l)} = \sum_{i=1}^{S^{(l)}} C_i^{(l)}$ is the total number of effective links between level l and $l-1$. This shows that the number of viable (or effective) links from level l to level $l-1$ must be smaller than the sum of the number of species in levels $l-1$ and l. On the other hand, the number of links between these two levels must be at least $S^{(l)}$ because each predator must have at least one prey, otherwise a predator has no resource and becomes extinct. Up to $S^{(l-1)}-1$ additional links can exist between these two layers. Moreover, if we consider only a part of the food web, the same conditions must hold for this part.

In addition to the $(C^{(l)} - S^{(l)})$ conditions resulting from equation (2.57), there are $S^{(l)}$ conditions resulting from the linear constraints and moreover $S^{(l)}$ conditions resulting from the condition fixed point condition of the population dynamics i.e., $G_i^{(l)}$ must vanish for each species in layer l. If we take the sum over all levels, we have in total

$$\sum_l \left(C^{(l)} + S^{(l)}\right) \equiv C + S$$

conditions for C efforts (total number of effective links) and S population sizes (total number of surviving species), as it must be.

If the network contains omnivores, we still have inequalities limiting the number of possible links. The most general expression for the restriction on the link number is $C^{(P,R')} < S^{(P)} + S^{(R')}$, where P is a set of species, R' is a subset of the prey set R of P (i.e., $R = \bigcup_{j\in P} R_j$, R_j is the set of prey of j). Therefore inequality (2.59) must hold even if there are omnivores regardless of the definitions of trophic levels. More generally, for all the "sub food webs", the condition (2.59) must hold.

With nonlinear constraints on the efforts, all efforts remain nonzero at the fixed point. For $r = 2$, the efforts was calculated analytically in the last section. The result was (2.45)

$$f_{ij} = \lambda_{ij} a_{ij} N_j / \sqrt{\sum_{j\in B_i} (\lambda_{ij} a_{ij} N_j)^2}\,. \tag{2.60}$$

This means that the effective connectance is identical to the potential connectance. However as nonlinearity r approaches one, we have more and more weak links at a fixed point, and at the limit $r \to 1$ we get the condition (2.59) (see also chapter 5).

Lotka-Volterra systems with other forms of competition

In the main body of this chapter, we are looking at the case where there is direct intraspecific competition but no interspecific competition. If the self competition β_i is set to be 0, we obtain a second set of inequalities in addition to (2.59), because the fixed point condition $G_i^{(l)} = 0$ is independent of $N_i^{(l)}$,

$$\sum_{j=1}^{S^{(l-1)}} \lambda_{ij} a_{ij}\, f_{ij} N_j^{(l-1)} - \sum_{k=1}^{S^{(l+1)}} a_{ki} f_{ki} N_k^{(l+1)} - \alpha = 0. \tag{2.61}$$

Since the variables f_{ki} and $N_k^{(l+1)}$ appear only in the combination $f_{ki} N_k^{(l+1)}$ in equation (2.61), we can define new variables $x_{ki} := f_{ki} N_k^{(l+1)}$ and obtain

$$\begin{aligned} \bar{g}_i \sum_{j=1}^{S^{(l-1)}} f_{ij} - \sum_{k=1}^{S^{(l+1)}} a_{ki} x_{ki} - \alpha = 0, \\ \bar{g}_i - \sum_{k=1}^{S^{(l+1)}} a_{ki} x_{ki} - \alpha = 0 \end{aligned} \tag{2.62}$$

for all prey j of species i. Thus, if we remember $\bar{g}_i = a_{ij} N_j^{(l-1)}$ for any j, we obtain a system of linear equations

$$a_{ij} N_j^{(l-1)} - \alpha - \sum_{k=1}^{S^{(l+1)}} a_{ki} x_{ki} = 0. \tag{2.63}$$

The variables in these equations are $N_j^{(l-1)}$ and x_{ki}. Hence there are $S^{(l-1)} + \sum_{k=1}^{S^{(l+1)}} C_k^{(l+1)}$ variables and $\sum_{i=1}^{S^{(l)}} C_i^{(l)}$ linear equations. In order that the system has a non-trivial solution,

$$C^{(l)} \le S^{(l-1)} + C^{(l+1)} \tag{2.64}$$

must hold. Especially, $C^{(L)} \leq S^{(L-1)}$ is valid for the top level L. Each species in level $L-1$ will be eaten by at most one species.

On the other hand, even when potential interspecific competition (2.51) is incorporated into the population dynamics, the condition (2.59) for the number of links does not change because the competition terms in this case do not affect foraging dynamics. However, if interspecific competition is defined in terms of effective connection, there is not a restriction on link structure any more. In subsection 3.1.4 in the next chapter, we will investigate the link structure of large webs with or without interspecific competitions by computer simulations.

2.2.3 Holling type II dynamics: diet selection

The inequality (2.59) followed from the linear dependence of the growth rate G_i on the efforts and population sizes. We therefore find a different result for Holling functional response. In this subsection, we only report on results for the model (2.12), and we keep the Holling patch choice model (2.14) for the next subsection.

We write the growth rate with (2.12) in the form

$$G_i^{(l)} = \frac{S_i}{1+T_i} - \sum_{k=1}^{S^{(l+1)}} \frac{a_{ki} f_{ki} N_k^{(l+1)}}{1+T_k} - \alpha - \beta N_i^{(l)}. \tag{2.65}$$

where

$$S_i = \sum_{j=1}^{S^{(l-1)}} \lambda_{ij} a_{ij} f_{ij} N_j^{(l-1)} \text{ and } T_i = \sum_{j=1}^{S^{(l-1)}} h_{ij} a_{ij} f_{ij} N_j^{(l-1)}.$$

The fixed point condition for adaptive dynamics is again

$$\partial G_i^{(l)} / \partial f_{ij} = \partial G_i^{(l)} / \partial f_{ij'}, \ (f_{ij} \neq 0, f_{ij'} \neq 0). \tag{2.66}$$

This does not yield linear equations any more, because $G_i^{(l)}$ is nonlinear. By applying the chain rule $\frac{\partial G_i^l}{\partial f_{ij}} = \frac{\partial G_i^l}{\partial S_i}\frac{\partial S_i}{\partial f_{ij}} + \frac{\partial G_i^l}{\partial T_i}\frac{\partial T_i}{\partial f_{ij}}$, we can explicitly represent Equation (2.66) as

$$\left(\lambda_{ij} a_{ij} + \frac{\partial G_i^{(l)} / \partial T_i}{\partial G_i^{(l)} / \partial S_i} h_{ij} a_{ij} \right) N_j^{(l-1)} =: \bar{g}_j \, . \tag{2.67}$$

Using

$$\frac{\partial G_i^{(l)} / \partial T_i}{\partial G_i^{(l)} / \partial S_i} = -\frac{S_i}{1+T_i}, \tag{2.68}$$

the fixed point condition of the population dynamics (2.65) gives

$$\frac{\partial G_i^{(l)} / \partial T_i}{\partial G_i^{(l)} / \partial S_i} = -\sum_{k=1}^{S^{(l+1)}} \frac{a_{ki} f_{ki} N_k^{(l+1)}}{1+T_k} - \alpha - \beta N_i^{(l)}. \tag{2.69}$$

The right-hand side is a function of the $N_k^{(l+1)}$ and the $N_i^{(l)}$ alone, making equation (2.67) a linear equation in $N_j^{(l-1)}$. However, the population sizes of the higher levels cannot be fixed independently of those at the lower levels, and we obtain no constraint of the type (2.59). Only if $\beta = 0$ do we obtain a constraint for the top levels: The right-hand side of Equation (2.69) is a constant if l is the top level, which leads to a linear set of equations (2.67) and to the condition (2.59) for the number of links between the upper two levels.

Therefore there is no mathematical reason why a constraint of the type (2.59) can be derived for Holling type II dynamics. For this reason, we performed simulations of small systems. We generated small food webs consisting of two predators, two prey, and one resource with fixed population size 1 using random values for the couplings chosen from the interval $[0, 1]$. We simulated the combined population and foraging dynamics with $\kappa = 2$. We chose $\lambda = 0.23$ which can be found for example in Krebs (2002) and found that for this value of λ the dynamics always reaches a fixed point. For larger values of λ, more complicated dynamics can arise. We fixed the initial population densities at 0.2 and 0.3 for predators and 0.8 and 0.6 for prey. Initial efforts are also fixed at 1/2. We considered species as being extinct when the population density dropped below 10^{-3} (extinction threshold) (Matsuda et al., 1996), and if a species died out, we generated a new system. If no species died out, we noted the link structure at the fixed point. Table 2.1 indicates how often each of the four possible link structures at the fixed point was obtained out of 1000 times. The handling times were chosen at random from the interval $[0, 0.02]$ for each simulation.

The result for the Holling model is shown in the second row in Table 2.1 together with Lotka-Volterra model. Comparing to the results of Matsuda et al. (1994) found for a Lotka-Volterra system (also shown in the first row in Table 2.1), we see that these results are similar in that the first link pattern (where both predators feed on the same and only one prey) is not frequently achieved. In the above parameter range, we were not able to numerically find the case of four links. Considering that the limit $h_{ij} \to 0$ leads to Lotka-Volterra systems, we expect that it should be more likely to find systems with four links when handling times are larger. Indeed, for larger values of handling times, we found systems with four links, however, the parameter range where they occur appears to be very small.

With nonlinear constraints on the efforts, all potential links are realized, i.e., the predators always feed on all their prey, albeit with a small rate if a prey population size is small. Our simulation of small systems confirms this conclusion.

Empirically, the number of links per species increases with the number of species in natural food webs. In most food webs, this linkage density is much higher than two as predicted by the Lotka-Volterra model with linear constraints (Martinez, 1992; Schmid-Araya et al., 2002; Brose et al., 2005; Dunne, 2006). These empirical findings are more consistent with the results presented here under a model with non-linear constraints.

In Figure 2.8, we show an example for the dynamics of a small system consisting of two predators, two preys and one resource with nonlinear and linear constraints. Four links are forbidden for the system with linear constraints (Matsuda and Namba, 1991; Matsuda et al., 1994; Matsuda et al., 1996), and here we

obtain four links at the fixed point only in the case of nonlinear constraints. For Holling type II dynamics (2.12), we find a similar behavior.

Figure 2.9 is an example of the same system as above, but the predator avoidance for the two preys is included. For linear constraints, both preys concentrate on foraging activity, and for nonlinear constraints, all the efforts remain nonzero.

2.2.4 Holling type II dynamics: patch choice models

The models for adaptive foraging considered so far could all be interpreted in terms of search images formed by predators, so that they search for a certain part of the time only for a certain type of prey. Part of them can also be interpreted as the predator spending a certain part of the time in a certain patch, where a certain prey is found. Here, we pursue the patch choice models further. We want to study systems with more than two trophic levels. This means that we have to specify the search behavior of a predator whose prey chooses between different patches. We can define two types of such multilevel patch choice models: In the first model, each species in each level is searched by its predator only in a given patch. This model is discussed briefly in the next subsection, and it resembles formally a lot the diet choice model. The main difference is that the death rate can be dependent on the patch, and therefore the death term becomes dependent on the efforts.

Clearly, this model has its limitations. A species is supposed to divide its time between different patches, where it finds different prey. However, the predators of this species are assumed to search for it in only one area. Even if we assume that this area is so large that it comprises all the patches the species moves through, the model would need some modifications in order to be more realistic. It should probably include larger overlaps (or larger exponents r in the constraint) for prey in higher trophic levels, and the predator success should depend on the foraging behavior of the prey. Alternatively, we discuss another patch choice model in the subsection after the next one. We divide space into patches according to the resources for the species at the lowest level. Predators on higher levels searching in one patch encounter a given prey with a probability proportional to the effort this prey puts into this patch. We will see that under certain conditions the populations in the different patches can be treated formally as independent species. This means that there are weaker constraints on link numbers than in the first model.

Each species has its own habitat

We first discuss the situation considered in Křivan (1996, 2003), Křivan and Schmitz (1996), Křivan and Sikder (1999), Baalen et al . (2001), Křivan and Eisner (2003), and Křivan and Diehl (2005), where each prey species has its specific habitat (or patch) (Brose, 2003; Tews et al., 2004). Each predator tries to maximize its energy intake by assigning time (effort) in the optimum way to the habitats of their prey species (Amarasekare, 2006). The model consequently resembles the diet choice model, with the only difference that death rates differ in different habitats.

The growth rate is in this case

$$G_i^{(l)} = \sum_{j=1}^{S^{(l-1)}} (\lambda_{ij}\, a_{ij} N_j^{(l-1)} - \alpha_{ij})\, f_{ij} - \sum_{k=1}^{S^{(l+1)}} a_{ki}\, f_{ki} N_k^{(l+1)} - \beta N_i^{(l)}. \tag{2.70}$$

Compared to the diet choice model, α_i is replaced with $\sum_{j=1}^{S^{(l-1)}} \alpha_{ij} f_{ij}$. The growth rate $G_i^{(l)}$ will now be maximized when

$$\lambda_{ij}\, a_{ij} N_j^{(l-1)} - \alpha_{ij} =: \bar{g} \tag{2.71}$$

holds for all prey j of i for which $f_{ij} \neq 0$. This set of equations is inhomogeneous, leading to the condition

$$C^{(l)} \leq S^{(l-1)} + S^{(l)} \tag{2.72}$$

instead of (2.59). Simulations of the two-predator two-prey model show that now four links can occur at the fixed point, see Table 2.1. For $\beta = 0$, we obtain equation (2.64), as for the diet choice model.

In Křivan (1997), patch choice with Holling type II functional response is considered. This is model (2.14), with α_i being replaced with $\sum_{j=1}^{S^{(l-1)}} \alpha_{ij} f_{ij}$. The energy intake is maximized if

$$\frac{\lambda_{ij} a_{ij} N_j^{(l-1)}}{1 + h_{ij} a_{ij} N_j^{(l-1)}} - \alpha_{ij} =: \bar{g}_i \tag{2.73}$$

is satisfied for all prey j of i for which $f_{ij} \neq 0$. We see that the simulation result shown in Table 2.1 (6th row) is similar to that of 5th row. Even when all death rates are equal (7th row), we cannot rule out the occurrence of 4 links, however, this was not observed for the parameter ranges used in the simulations.

Common habitats

Now let us assume that there are in total M patches, between which all species in the community move. Each species i tries to maximize its growth rate by spending the appropriate proportion of time in each patch m. We will see that in the absence of a competition term the populations in the different patches decouple, and the community in each patch can be considered independently. We will also find that if the death rate does not depend on the patch the species in the second level from above spend the same time in each of those patches where they can be found.

We consider here a 3-level system of plants (indexed by $j = 1, \cdots, J$), herbivores (indexed by $i = 1, \cdots, I$) and carnivores (indexed by $k = 1, \cdots, K$), and suppose that there are M useful patches (indexed by $m = 1, \cdots, M$). Each species optimizes its energy intake through its optimal habitat choice. We denote the population of each consumer species by $N_s, (s = i, k)$, and the proportion of (or fraction of time spent by) species N_k, N_i in patch m by y_{km}, x_{im} respectively, and the population of each plant in patch m by N_{jm}, and its growth term by E_{jm}. Thus we have

$\sum_m y_{km} = 1$ and $\sum_m x_{im} = 1$. Then the population dynamics with Lotka-Volterra functional response is

$$\begin{aligned}
\frac{dN_k}{dt} &= N_k(\sum_{i=1}^{I} \lambda_{ki} a_{ki} \sum_m^M y_{km}(x_{im}N_i) - \sum_m^M \alpha_{km} y_{km} - \beta N_k), \\
\frac{dN_i}{dt} &= N_i(\sum_{j=1}^{J} \lambda_{ij} a_{ij} \sum_m^M x_{im} N_{jm} - \sum_{k=1}^{K} a_{ki} \sum_m^M x_{im}(y_{km}N_k) - \sum_m^M \alpha_{im} x_{im} - \beta N_i), \\
\frac{dN_{jm}}{dt} &= N_{jm}(E_{jm} - \sum_{i=1}^{I} a_{ij}(x_{im}N_i) - \beta N_{jm})\,. \qquad (2.74)
\end{aligned}$$

If the competition for resources other than food does not affect population dynamics, the last term in the first two equations can be dropped. Introducing $N_{km} = y_{km}N_k$ and $N_{im} = x_{im}N_i$, we then obtain for the first two equations

$$\begin{aligned}
\frac{dN_k}{dt} &= \sum_m^M N_{km} \left(\sum_{i=1}^{I} \lambda_{ki} a_{ki} N_{ki} - \alpha_{km} \right), \\
\frac{dN_i}{dt} &= \sum_m^M N_{im} \left(\sum_{j=1}^{J} \lambda_{ij} a_{ij} N_{jm} - \sum_{k=1}^{K} a_{ki} N_{km} - \alpha_{im} \right), \qquad (2.75)
\end{aligned}$$

which shows that the growth rate of a species is the sum of the growth rates of its populations in the different patches. The food web is identical to a set of independent food webs in different patches, without adaptive foraging. Independent population dynamics in each patch leads to exactly the same fixed points as adaptive foraging between different patches.

Let as now assume $\beta \neq 0$ and explore the consequences of adaptive dynamics. Maximizing the growth rate of carnivores and herbivores gives the conditions

$$\begin{aligned}
\sum_{i=1}^{I} \lambda_{ki} a_{ki} x_{im} N_i - \alpha_{km} &=: \gamma_k \qquad (2.76) \\
\sum_j \lambda_{ij} a_{ij} N_{jm} - \sum_{k=1}^{K} a_{ki} y_{km} N_k - \alpha_{ki} &=: \gamma_i
\end{aligned}$$

for all those patches m where the species k (first equation) or i (second equation) are found. If the death rate is independent of the patch, the x_{im} is the only m-dependent quantity in the first set of equations. As we will show in the next paragraph, the population sizes are determined independently of the efforts, leaving the x_{im} as the only variables in the first equation. For $I \geq K$, the solution $x_{im} = x_{im'}$ is the only one for all patches m, m' where species i is found. Predation leads to an equal distribution of the species in the second level from above between the different patches if there are at least as many carnivore species as herbivore species. This is plausible, since a predator will put more effort into a patch with more prey, until the prey population size is equal in all patches. If the carnivore death rates

depend on the patch, equation (2.76) still determines the x_{im}, which are however no longer identical.

Let us now determine the conditions for the population sizes. Inserting conditions (2.76) into the population dynamics (2.74) for carnivores and herbivores, we obtain

$$\begin{aligned} \frac{dN_k}{dt} &= N_k(\gamma_k - \beta N_k), \\ \frac{dN_i}{dt} &= N_i(\gamma_i - \beta N_i), \end{aligned} \tag{2.77}$$

giving $\gamma_k = \beta N_k$ and $\gamma_i = \beta N_i$ at the fixed point. Inserting this result into equations (2.76) and performing the sum over m, we obtain $I + K$ equations for the $I + K$ population sizes of carnivores and herbivores, which are independent of the efforts x_{im} and y_{km}. This fixes the population sizes, and equations (2.76) can be understood as equations for the efforts alone.

The link statistics for systems with two patches with one plant species each, two herbivores and two carnivores is shown in the last row of Table 2.1 for the case of equal death rates. Four links between carnivores and herbivores are achieved only in 13 percent of the systems.

Our results imply that using efforts into patches instead of efforts into prey leads to less restrictions on link numbers, even if constraints are linear. The model presented in this subsection allows that predators still encounter other prey while searching for a given prey. This is what motivated our introduction of nonlinear constraints on the foraging efforts. It now appears that efforts into patches with linear constraints can achieve the same goal.

2.3 Conclusion

We have investigated mainly analytically the link structure and the survival chances of prey species of food webs with different types of population dynamics and different types of adaptive dynamics. The results depend strongly on the type of population dynamics and the model of adaptive behavior used.

In terms of stability, we have shown that the adaptive foraging enhances the persistence of a prey with a small population size. However, the standard implementation of adaptive foraging, which uses linear constraints on the efforts, has the drawback that it leads to unrealistically small link numbers in food webs. That is, we have for Lotka-Volterra dynamics the restriction that the sum of links of two neighboring levels cannot be larger than the sum of species in these two levels. The high number of trophic links found in natural food webs (Martinez, 1992; Schmid-Araya et al., 2002; Brose et al., 2005; Dunne, 2006) is more consistent with the predictions of the nonlinear model. This can be rigorously shown for Lotka-Volterra models, and appears to be also true for a large part of the parameter space of Holling type II models. We have argued in this chapter that using nonlinear constraints on the efforts can be motivated from ecology much better than linear

constraints, and that it allows for the large link numbers found in nature. Using patch choice models where higher-level predators choose patches and not prey, has a similar effect. We therefore suggest that in theoretical investigations where link numbers are important, nonlinear population growth and nonlinear constraints on efforts should be used.

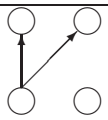
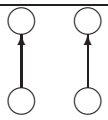
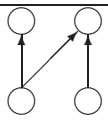
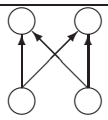
In the absence of a intraspecific competition term (where population dynamics becomes linear also in the considered population size), there is an additional constraint which becomes most relevant for the two top levels, where each prey can at most be taken by one top predator. Such constraints cannot be derived for Holling type II dynamics. Nevertheless, computer simulations of small model food webs show similar results for the link numbers of the Holling and the Lotka-Volterra systems, indicating that larger link numbers are achieved only for a small part of parameter space.

We also explored the consequences of abandoning the linearity of the constraints for the efforts. We found that for nonlinear constraints all possible links are present, even if very weak for very small prey population size. Nevertheless, nonlinear constraints for the efforts still allow small prey populations to survive as long as they have enough food and as long as their predators have other, more abundant prey. The stabilizing effect found for linear constraints therefore exists also for nonlinear constraints on the efforts.

When adaptive behavior comprises predator avoidance as well as adaptive foraging, linear (Lotka-Volterra) population dynamics leads to the result that it pays never off to put effort into predator avoidance. Only when the growth term is a nonlinear function of food intake does predator avoidance become profitable. Empirically, predator avoidance behavior has been documented for many predator-prey interactions in various ecosystem types (Loose and Dawidowicz, 1994; Peckarsky, 1996; Turner et al., 2000). Again, this is more consistent with the findings obtained using the nonlinear model.

Finally, we studied models where space is divided into patches, between which consumers divide their foraging time. Under certain conditions, this leads to an equal distribution between patches of the species in the second layer from above. In the absence of direct competition between consumers, such a system is formally equivalent to a set of independent systems that do not contain adaptive foraging. More interestingly, assigning efforts to patches instead of prey, has a similar effect on link numbers as using nonlinear constraints on efforts into prey.

Table 2.1: Frequency of different link structures obtained with different population and foraging dynamics for a system of two predators, two prey, and one resource, in the case where all four species survive

Link Structure[a]	 2a	 2b	 3	 4
1 Diet choice, L-V[b], Linear	55	499	446	0
2 Diet choice, H[b], Linear	48	643	309	0
3 Diet choice, L-V, Nonlinear	0	0	0	1000
4 Diet choice, H, Nonlinear	0	0	0	1000
5 Patch choice, L-V	41	480	473	6
6 Patch choice, H	31	483	481	5
7 Patch choice (id. death rates), H	43	385	572	0
8 Patch choice (same habitat)	289	97	488	126

[a] Link structure 2a indicates that the two predators finally feed on the same prey. Number 2b means that one predator feeds on one prey and the other predator feeds on the other prey. In both cases, there are in total 2 links between predators and preys. In the cases 3 and 4 there are 3 and 4 links.
[b] L-V and H are abbreviations for Lotka-Volterra and Holling functional responses respectively.

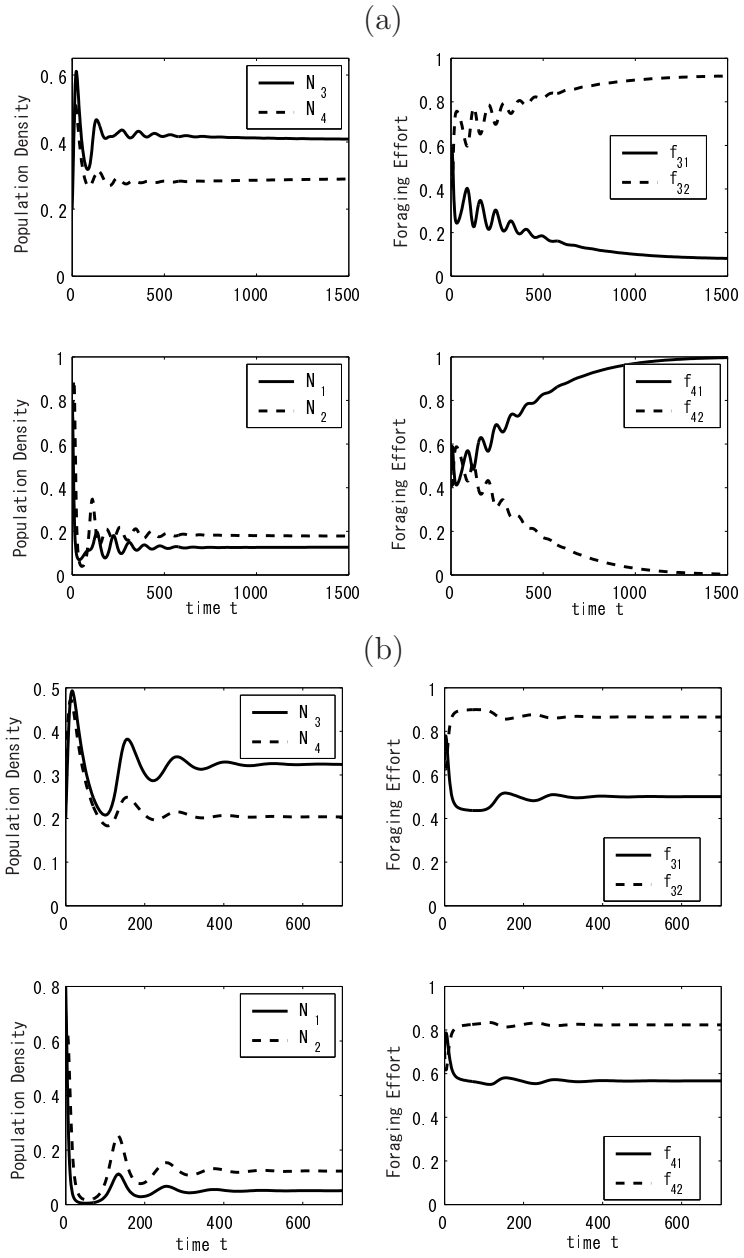


Figure 2.8: (a): Time series of the four populations (left figures) and foraging efforts (right figures) for the model with Lotka-Volterra functional response with linear constraints on the efforts. N_1 and N_2 are population densities of the bottom species, N_3 and N_4 are those of the top species. f_{ij} denotes the foraging effort species i invests in species j. The values of the couplings between predators and prey are $a_{11} = 0.7, a_{12} = 0.3, a_{21} = 0.5, a_{22} = 0.3$, and between the prey species and the resource, $a_{10} = 0.8, a_{20} = 0.9$. All these values were chosen at random. Other parameter values are fixed at $\alpha_1 = 0.01, \alpha_2 = 0.0001, \beta = 0.05, \lambda = 0, 23, \kappa = 2$. (b): Same as (a), but with nonlinear constraints on the efforts.

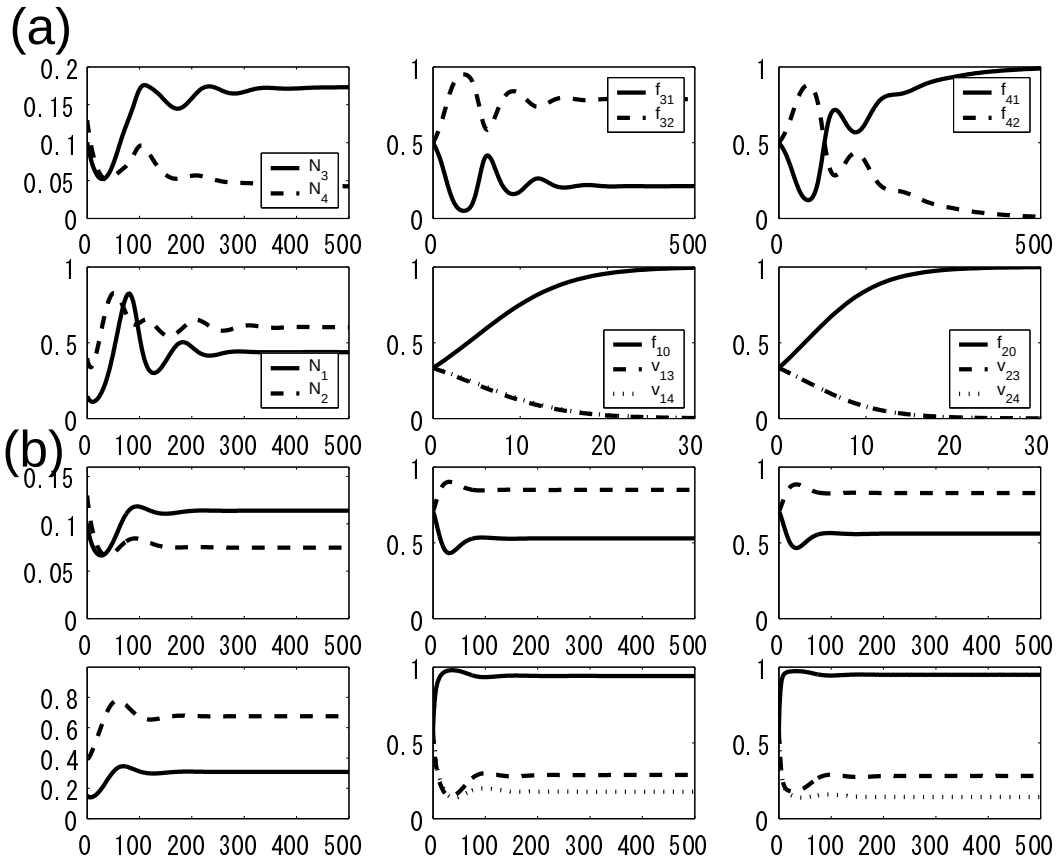


Figure 2.9: (a): Time series of the four populations, foraging efforts and predator avoidance for the model with Lotka-Volterra functional response with linear constraints on the efforts. All the parameter values are same as Figure 2.8. (b): Same as (a), but with nonlinear constraints on the efforts.

Chapter 3

Community Persistence and Web Structure

In this chapter, we present our simulation results for the food web robustness as function of connectance, initial species number and average number of prey per species. We also present results for the species deletion stability, the number of effective links, and the trophic structure of the webs resulting after population dynamics. The implications of these results are discussed in the last section.

3.1 The model used in simulations

3.1.1 Dynamics

The dynamics used here is based on the model (2.1):

$$\frac{dN_i(t)}{dt} = \sum_{j\in B_i} \lambda_{ij} g_{ij}(t) N_i(t) - \sum_{k\in R_i} g_{ki}(t) N_k(t) - \alpha_i N_i(t) - \beta_i N_i^2(t).$$

The most general expression for the functional response is

$$g_{ij}(t) = \frac{a_{ij} f_{ij}(t)(1 - v_{ji}(t))N_j(t)}{1 + \sum_{j'\in B_i} h_{ij'} a_{ij'} f_{ij'}(t)(1 - v_{j'i}(t))N_{j'}(t)}. \tag{3.1}$$

Potential connection strengths a_{ij} take a positive value if i is a predator of j, and are zero otherwise (how this connection pattern is determined is explained in the next subsection). The values of a_{ij} (if they are nonzero) are chosen randomly from the interval $(0, A)$. We can set $A = 1$ without loss of generality, because this situation can always be achieved by rescaling the parameters according to $a'_{ij} = a_{ij}/A, \alpha' = \alpha/A, \beta' = \beta/A, h'_{ij'} = Ah_{ij'}, t' = At$. $h_{ij'}$ is the handling time. In our simulations the values of the handling time are randomly chosen from the range $(0, 0.02)$. If all the values $h_{ij'}$ are set to zero, g_{ij} leads to a functional response of Lotka-Volterra type, which we also used in our simulations. The factor λ_{ij} in the first term is the ecological efficiency, for which we chose the value 0.23 suggested by Krebs (2002) for all the species. We chose the values $\alpha_i = 0.05$ and $\beta_i = 0.4$.

The variable $f_{ij}(t)$ is the effort species i spends on foraging for prey species j, and $v_{ji}(t)$ is the effort species j spends on avoiding predator i. Both types of efforts take values in the interval $[0, 1]$. If $f_{ij}(t) = 0$ or if $v_{ji}(t) = 1$ no energy flows from j to i. In this sense we call $a'_{ij} = a_{ij} f_{ij}(t)(1 - v_{ji}(t))$ the effective connection strength between i and j.

By writing $x_{il} = f_{ij}$ for $l = 1, \cdots, B_i$ and $x_{il} = v_{ik}$ for $l = B_i + 1, \cdots, B_i + R_i$, the dynamics for adaptive behavior is implemented by the equation

$$\frac{dx_{il}(t)}{dt} = \kappa x_{il}(x_{il}^{1-r} \partial G_i/\partial x_{il} - < \partial G_i/\partial x_{il} >), \tag{3.2}$$

with nonlinear constraints

$$\sum_{j \in B_i} f_{ij}(t)^r + \sum_{k \in R_i} v_{ik}(t)^r = 1 \tag{3.3}$$

with an exponent r larger than 1 (chapter 2). The function G_i is the growth rate of species i ($dN_i/dt = G_i N_i$). The last expression in the previous equation is

$$\langle \partial G_i/\partial x_{il} \rangle = \sum_{j \in B_i} f_{ij} \partial G_i/\partial f_{ij} + \sum_{k \in R_i} v_{ik} \partial G_i/\partial v_{ik} \, .$$

The parameter κ sets the time scale of the adaptative dynamics compared to that of the population dynamics. We assumed that the changes of the behavior are faster than the population dynamics in contrast to the papers of Brose et al. (2003) and Kondoh (2003, 2006), and we therefore set $\kappa = 2$ in our simulations. Efforts that have become zero cannot increase again according to equation (3.2). We therefore set the value of an effort that has become smaller than 10^{-4} to the value 10^{-4}, so that it can increase again later.

Let us first summarize briefly what we know about the properties of Lotka-Volterra dynamics combined with linear constraints as discussed in chapter 2:

First, there exist no fixed points of the dynamics with nonzero predator avoidance efforts if foraging efforts are included in the model. For this reason, the model with linear constraints should be considered with foraging efforts only or with predator avoidance efforts only. For nonlinear constraints, both types of efforts can simultaneously be nonzero.

Second, linear constraints on the foraging efforts (in a model with foraging efforts only) leads to fixed points where the number of nonzero efforts must be smaller than the sum of the numbers of all predators and all prey species. This means that the total number of effective links must be smaller than twice the number of species in the system. Similarly, in a model with predator avoidance efforts only, the total number of nonzero predator avoidance efforts must be smaller than twice the number of species.

For Holling functional response, this condition is not valid any more, however, the range of parameter values where more nonzero efforts than predicted by this condition are found, is small. In fact, all simulation results presented in the next section look very similar for Lotka-Volterra and for Holling type II functional response, and we will therefore show only results obtained with Lotka-Volterra functional response.

3.1.2 Prey-predator relations

To determine the connection pattern of webs (i.e., zero-nonzero pattern of potential connection strength a_{ij} or equivalently B_i for all i), we use a random topology and a topology obtained from the niche model (Williams and Martinez, 2000, 2004). To produce random webs, we assign a nonzero value to a_{ij} for a pair of species in species set (i, j) with probability C. If this has happened, $j \in B_i$. C is called connectance of webs. It should be noted that B_i can contain i (cannibalisms). For Lotka-Volterrs systems with adaptive foraging, the effective strangth a'_{ii} always disappears, even if $a_{ii} > 0$, because the potential pay-off $\partial G_i/\partial f_{ii}$ is always negative. For Lotka-Volterra systems without adaptive foraging, the effect of a_{ii} can be absorbed into intraspecific competition by $\beta'_i = \beta_i + (1 - \lambda_{ii})a_{ii}$. For Holling type II functional response, the effect is not trivial. However, the results of simulations do not depend on whether we include cannibalisms into the model or not.

To produce niche webs, we used the algorithm proposed in Williams and Martinez (2000). It is recognized that the niche model produces web structures (i.e., connection patterns) similar to those of real food webs. This model assumes that a particular arrangement of a one dimensional space (called niche space), where all the species in a web are located, determines prey-predator relations in food webs (Figure 3.1). Each species is assigned three random parameter values $n_i \in [0, 1]$ (niche value i.e., position in the niche space) and $[q_i, Q_i]$ with $q_i < 1, q_i < Q_i < 1$ (feeding range in the niche space i.e., i feeds on j if $n_j \in [q_i, Q_i]$). By specifying these parameter values, the web pattern is determined. The niche value n_i is chosen uniformly and has the mean value 1/2. The model does not directly determine the feeding range but assigns the relative width $r_i = (Q_i - q_i)/n_i$ and the center $c_i = (Q_i + q_i)/2$ of feeding range. The relative width r_i is specified by the beta distribution with shape parameter $\alpha = 1$

$$P(r|\alpha = 1, \beta) = \beta(1 - r)^{\beta-1}. \quad 0 \leq r \leq 1 \tag{3.4}$$

Therefore the mean value of the relative width $\langle r_i \rangle = \frac{1}{1+\beta}$ and the mean value of the width $\langle Q_i - q_i \rangle = \langle n_i \rangle \cdot \langle r_i \rangle = \frac{1}{2+2\beta}$, which is connectance C. Positive β restricts the connectance $C < 1/2$, and, for $C < 1/4$, the beta distribution is a monotonically decreasing function. Then the feeding center is chosen uniformly from the interval $[\frac{n_i r_i}{2}, n_i]$, i.e, the minimum value of the feeding center is the half of the feeding width so that q_i is always positive and the maximum is the niche value so that species i is more likely to feed on species with smaller niche values than those with larger niche values.

For both types of webs, the prey set B_i can include external resources, whose sizes are assumed to be constant and which do not feed on any species. For random webs constructed by $S + E$ species, E species are simply chosen at random as external resources. For niche webs, species are ranked by niche values and we regard the species with the E smallest niche values from $S + E$ species as external resources. From now on, we call these E species "external resources" and other S species "species".

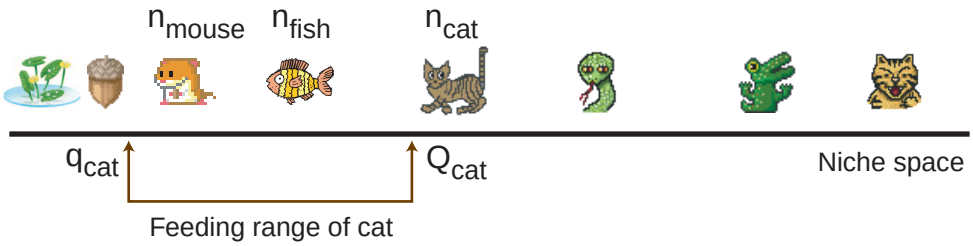


Figure 3.1: Species on a niche space.

3.2 Simulation results

In order to evaluate the stability of model food webs, we first generated a web topology and assigned values of the connection strength. Connections were chosen such that each species has at least one prey. In all the simulations we fixed the number of external resources, E at 2, and their sizes were kept at the constant values 5 and 6. (Note: "the population sizes" N_i are in fact the total biomass of a species, measured in convenient units, which should not be understood as the number of individuals of a species. Since we consider species with a biomass below 10^{-3} as extinct (see below) , a size of the order 1 is in fact large.)

Then, we applied the population dynamics. We investigated four kinds of dynamics:

(a) Classical population dynamics.

This does not include any foraging behavior of species. The functional response is given by $g_{ij}(t) = \frac{a_{ij}N_j(t)}{1+\sum_{i'\in B_i} h_{ii'}a_{ii'}N_{i'}(t)}$ (which is equation (2.3)) without the factors containing the efforts), and the values of the connection strength a_{ij} are assigned at random from the interval $(0, 1)$.

(b) Population dynamics without adaptive behavior.

In this case, we have $\kappa = 0$, and the effective connection strength is given by $a_{ij}f_{ij}(0)$ for all times, where $f_{ij}(0) = 1/|B_i|$ and $|B_i|$ denotes the number of prey of i.

(c) Population dynamics with adaptive foraging (linear constraints).

(d) Population dynamics with adaptive foraging (nonlinear constraints).

We notice here that in the cases (b) and (c) the average of the sum of (effective) connection strength is independent of the number of prey $|B_i|$:

$$\langle \sum_{j\in B_i} a_{ij}f_{ij} \rangle = \langle a_{ij} \rangle = 1/2, \tag{3.5}$$

while in the cases (a) and (d) the average of the sum depends on the number of prey. In case (d), however, the sum given in equation (3.3) does not depend on the number of prey.

Whether the dynamics leads to a fixed point, a limit cycle or a chaotic attractor depends on the parameter values (see also Williams and Martinez, 2004), especially on the conversion efficiency λ and the handling time h. For the value $\lambda = 0.23$ chosen by us, the dynamics always reached a fixed point, usually with

several species having become extinct, because their biomass reached zero (In all the simulations we considered a species as extinct if the biomass of the species dropped below 10^{-3}). At this fixed point, the resulting web was then evaluated. We evaluated four different features of the resulting webs.

First, we evaluated the robustness, i.e., the proportion of species that have survived. If S denotes the initial number of species and S' the number of species with nonzero biomass after running the population dynamics, the robustness is given by S'/S.

Second, we evaluated the species deletion stability. We deleted a randomly chosen (surviving) species (not the external resources) from the web, did another run of the population dynamics until again a fixed point was reached, and counted the number S'' of species present at the end. The species deletion stability is defined as $S''/(S'-1)$.

Third, we evaluated the (final) connectance of the resulting webs, counting potential links, i.e., links defined by a nonzero connection strength a_{ij}, and effective links, which are links with nonzero efforts (i.e., efforts larger than 10^{-4}). The final connectance is defined as the number of links divided by the number $(S'+E)S'$ of pairs of species.

Fourth, we evaluated the trophic structure of the resulting webs, counting the number of species on each trophic level. We defined the trophic level of a species as the shortest chain length from a resource to this species, going through potential links.

We did not investigate the second and third properties for the case (b), because, as is shown in the next subsection, the robustness is too small to obtain sufficiently large webs after population dynamics (see Figure 3.2) to study these properties.

3.2.1 Robustness

Figure 3.2 shows our results for the robustness as function of the connectance C for fixed initial species number $S = 40$, for the robustness as function of initial species number S at fixed connectance $C = 0.2$, and for the robustness as function of initial species number S at fixed number of prey $K = 4$ per species.

We notice that the number of external resources E is always fixed at 2 even when the robustness is estimated as a function of S. If we do so, for random webs, the average energy input from resources to a species depends only on C and is independent of S, because the average number of connections from E resources to a species is given by the product CE and the sizes of resources are fixed. We also fixed the number of external resources for niche webs to compare the results with those of random webs. Actually, according to numerical calculations, the absolute number of species that feed on the external resources increases as S for fixed C (see also Figure 3.6 (1), (4)).

Data are averaged over 1000 webs. We found in our simulations that the relation between robustness and C, S and K is not affected by the sizes of the resources. No predator avoidance was included in these simulations.

We can discern the following features of the data:

- Robustness is always higher with adaptive foraging (the cases (c),(d)) than without adaptive foraging (the cases (a),(b)). With adaptive foraging, it increases with increasing connectance C, as was found by Kondoh (2003). Without adaptive foraging, the robustness takes a maximal value at some small connectance and decreases with increasing connectance C for random webs. For the case (a), this value is about 0.15 and for the case (b), 0.35. These increases seen for small values of C in the random model are due to the decrease of the number of species that are not part of a food chain going down to the resources. In fact, the robustness must be zero at $C = 0$. Especially for the case (a), it decreases with increasing connectance, as is known since the work of May (1972).

- When the species number is increased at fixed connectance and with adaptive foraging, the robustness increases slowly for the random model, but decreases for the niche model.

- When the number of prey per species, K is fixed, the robustness decreases always with increasing S. Since $K = (S + E)C$, the number of prey per species increased in the previous two cases.

- Robustness is always larger for case (a) than for case (b). Because the average connection strength is larger for (b) than for (a) ($a_{ij} \geq a_{ij} f_{ij}$), these results are contrast to what one might expect, knowing that usually weak links are stabilizers of food webs. Apparently, if all links are weak (and not only part of the links), food webs are again less stable (Csermely, 2006).

- Robustness is slightly smaller when the constraints on the efforts are nonlinear, compared to linear constraints. We have chosen the exponent r in equation (3.3) equal to 2 (linear constraints correspond to $r = 1$). For $r \to \infty$, dynamics with and without adaptive foraging become the same (chapter 2), and we therefore expect a decrease in robustness with increasing r.

Taking all these results together, we conclude that increasing the number of prey per species increases robustness in the presence of adaptive foraging, since species can better survive if they can choose among more prey. This is true also for the niche model, if the number of resources is kept constant. Our results shown here agree in this point with the claim by Kondoh (2006).

However, increasing the number of species decreases robustness. This is true even with adaptive foraging. If the number of prey per species and the number of species are increased at the same time (as is the case when S is increased at fixed C), the net effect can be an increase or a decrease of the robustness, depending on the web structure. For the niche model, the destabilizing effect of an increase in species number appears to be larger than for the random model. This can be due to the fact that in the niche model species that have similar niche values tend to share the same predators, since they are likely to fall within the same feeding ranges.

We also investigated the effect of predator avoidance behavior on the robustness as a function of C (not shown). Avoidance behavior leads to a somewhat increased

robustness, but does not change the trends present without avoidance behavior. With linear constraints, the increase in robustness becomes very small for larger C or K, due to the above mentioned restriction that the total number of nonzero predator avoidance efforts must be smaller than twice the number of species in the network.

As was done by other authors, the interspeciefic competition was not included in our simulations. If we try to incorporate the interspecific competition into the adaptive foraging model, there are 2 possibilities as was discussed in subsection 2.1.5 of the last chapter. We investigated the effects of both competition types on the robustness for the foraging dynamics. Figure 3.3 is the data same as Figure 3.2, but here the interspecific competition is taken into account. The strength of competition $\sigma = 1$, which assumes the most harsh case for the interspecific competition. If the potential competition is taken into account, the positive relations for all the cases are broken. This effect is because, as we concluded, the number of potential prey (or the number of potential links) plays an important role in foraging dynamics. On the other hand, increasing the number of potential prey increases the number of competing species. And from the figure, we find that the positive effect by increasing the number of potential prey cannot compensate the negative effect by increasing competition. But if we assume the niche segregation in the model, i.e., the competition is defined by effective links, the positive relation is recovered as a function of connectance C.

3.2.2 Species deletion stability

Our results for the species deletion stability are shown in Figure 3.4. The ranges of x-axes for the top figures ((1),(3)) and the bottom figures ((2),(4)) are different, because for case (a) it is difficult to find large food webs ($S' > 18$) after population dynamics. For random networks, the trends are exactly the same as for the robustness: without adaptive foraging (case (a)), increasing C or increasing the species number leads to less stability, and with adaptive foraging to more stability. In the niche model, networks are more stable with adaptive foraging than without adaptive foraging, however, an increasing species number appears to have a stabilizing effect now, in contrast to the robustness simulations. We believe that this is due to the fact that deletion of a species affects a smaller proportion of the network when the network is larger. Instead, an increase in connectivity does not lead to more stability. An increase in connectivity has the advantage that species can choose among more prey, but the disadvantage that a change at one place in the network is felt by more species. For the niche model, these two effects appear to cancel each other.

3.2.3 Initial and final connectance

We investigated the initial and final connectance (connectance after population dynamics) of webs. As we have pointed out above, the effective connectance is much smaller than the potential connectance in the presence of adaptive foraging with linear constraints on the efforts. This is because many efforts become zero. With

nonlinear constraints on the efforts, efforts can become small but usually remain nonzero. We evaluated the effective and potential connectance of food webs with linear constraints on the efforts after population dynamics. The results are shown in Figure 3.5 as a function of the (potential) connectance of the initial web. The potential final connectance is almost identical to the initial connectance for random webs and is larger than the initial connectance for niche webs, while the effective final connectances are small for both webs. The effective connectance for random webs becomes independent of the initial connectance in the region where the initial connectance is large, and the effective connectance for niche webs decreases with the initial connectance for the shown parameter region. In producing niche webs, we restricted the value of the parameter C to the interval $[0.1, 0.5)$.

For smaller values of the initial connectance the final (potential) connectance is larger than the initial connectance in both models, because all species that are not part of a food chain to a resource are eliminated by the population dynamics, leaving a network with more connections. This happens easier for niche webs.

The result for the effective final connectance for linear constraints can be understood quantitatively. As mentioned earlier, there is a restriction on the total number of effective links, which must be smaller than twice the number of species. If the maximal connection number ($L = 2S' + E - 1$) is achieved, the connectance takes the value $(2S' + E - 1)/(S' + E)S'$. For larger initial connectance, almost all species survive under population dynamics with foraging behavior (Figure 1), and the maximal effective connectance is obtained as 0.048 for $S' = 40, E = 2$. which is close to the value seen in our simulations. For niche webs, S' increases with the initial connectance, and therefore the effective connectance $\leq (2S' + E - 1)/(S' + E)S' = (2S' + 1)/(S' + E)S' \simeq 2/(S' + 2)$ decreases.

For the cases (a) and (d), the final connectance are almost identical to the initial connectance, even though, especially for the case (a), increasing connectance increases the robustness.

We also investigated the average (potential) connection strength after population dynamics, and found that, for all cases we investigated, the average final connection strength is almost identical to the average initial connection strength $\langle a_{ij} \rangle = 0.5$.

This result holds even if we include the potential competition into the model, because in this case the potential competition does not affect the foraging dynamics that restricts the effective connection pattern of food webs. As discussed in chapter 2, we expect that the effective competition breaks these restrictions, because there is no mathematical reason any more why the effective connectance must be restricted (subsection 2.2.2). However, even in that case, we have found that the final effective connectance is as small as in the case where no interspecific competition is included. This is a result of the niche segregation and competition avoidance, which is another mechanism from the foraging model without competition: if the effective connectance is large, then the competition among species is also large, however this situation will be avoided by the competition avoidance behavior.

3.2.4 Trophic level structure

Finally, we show the trophic level structure of the models in Figure 3.6. We define the trophic level of a species as the shortest path to the external resources. For example if a species feeds directly on an external resource, the level of the species is one. This definition of the trophic level is also called the shortest chain length. For random webs, the initial number of species in trophic level l is $n^{(l)} = S((1-C)^{S^{(l-2)}} - (1-C)^{S^{(l-1)}})$ with $S^{(l)} = \sum_{m=0}^{l} n^{(m)}$ and with $n^{(0)} = E$. This can be understood by realizing that the probability that a species has a link to a species in the first l levels is $1-(1-C)^{S^{(l)}}$.

The top two graphs in Figure 3.6 ((1),(4)) show the initial structures of random and niche webs. For both webs there are more species in the middle levels for sufficiently large systems ($S > 15$). The number of species in higher trophic levels (only level 3 is shown in the figures) increases with the system size S for niche webs. However, this trend must be reversed when S increases beyond the range of values shown in the Figure, since in the limit $S \to \infty$ only two trophic levels can exist for both types of webs. The reason is the following: if we fix C, a species is connected to an increasing number CS of other species when S increases. Furthermore, a nonvanishing proportion p of all species are in level 1. Therefore the probability that a species is not connected to a species in level 1, which is given by $(1-p)^{CS}$ decreases to zero when S goes to infinity. For the niche model, p depends on the niche value, but is nonzero along the entire niche axis, and therefore the argument applies also to the niche model.

The middle and bottom graphs ((2),(3),(5),(6)) show the trophic level structure after dynamics for the case (a) and case (c). For the resource sizes 5 and 6 used in all our simulations, the number of trophic levels is preserved during dynamics. However, for random webs without foraging dynamics (2) there are many species in lower trophic levels at the end. This can be understood by the following argument: for niche webs, species are ranked by niche values and species with larger niche values tend to belong to larger trophic levels. And it is more difficult that a species with a smaller niche value feeds on a species with a larger niche value than that a species with a larger niche value feeds on a species with a smaller niche value. Thus, energy tends to flow from species with smaller niche values to those with larger niche values as a whole. In contrast to this, random webs do not have any preferred direction for the link between two species. Therefore, for random webs, the energy from resources is not efficiently transported to higher levels. With adaptive foraging, the final trophic level structure is almost identical to the initial structure for both random and niche webs (bottom figures (3),(6)). The trophic levels shown in the figure are evaluated based on effective connections after dynamics. However, there are not large differences if we evaluate the trophic level structure by using potential connections. The stability of the higher levels can be explained as follows: A species with foraging behavior can choose a prey with a large biomass. Because the conversion efficiency λ is smaller than one, we can expect that a species in higher levels has usually a smaller biomass than a species in lower levels. Thus, a species tends to stop feeding on species in higher trophic levels, allowing the species in higher levels to survive more easily. We also

investigated the dependence of our results on the sizes of resources. When the sizes of the external resources are 1.0 and 1.2, there are only two trophic levels after population dynamics instead of three levels.

For the case (d) (population dynamics with foraging dynamics with nonlinear constraints), the trophic level structure is almost identical to the trophic level evaluated by going also through potential connections. And for the case (b), we have only the first trophic level.

3.3 Conclusion

In this chapter, we have investigated the influence of topology (random or niche model), population dynamics (Lotka-Volterra or Holling) and individual adaptive behavior (foraging behavior and/or predator avoidance behavior with linear or nonlinear constraints) on the stability and structure of food webs. We showed that a positive complexity-stability relationship is obtained with adaptive foraging in all types of networks studied. The stabilizing effect of foraging dynamics as species number and connectivity increase, is due to the increasing number of potential prey per species, as can be concluded from Figure 1. Predator avoidance behavior does not cause a qualitative change in the stability. Foraging dynamics with linear and nonlinear constraints leads to similar results, with the exception of the effective connectance, which is constant (at fixed connectivity and as function of species number) for large webs with linear constrains, and proportional to the potential connectance for nonlinear constraints. With nonlinear constraints, food webs are therefore "complex" even when the effective connectance is considered, and we consider this type of constraints more realistic than linear constraints, since it takes into account the effect of accidental feeding.

Species in higher trophic levels can survive under dynamics only if the external resources are sufficiently large. Survival on higher levels is easier in niche webs than in random webs. However, the situation investigated in this chapter and in most other paper on the topic is somewhat artificial since the initial web configuration is generated ad-hoc. Ultimately, model food webs and the analysis of their stability should be based on some type of evolutionary dynamics that generates the web structure by an iterated process of invasions and/or speciation events, such as in Bastolla et al. (2001) and Drossel et al. (2001) as discussed in chapter 1. Such models allow for a wider range of stability criteria, since the stability of the topological structure under long-term changes of the web composition can also be considered. Evolutionary models combined to adaptive foraging dynamics are investigated in chapter 5.

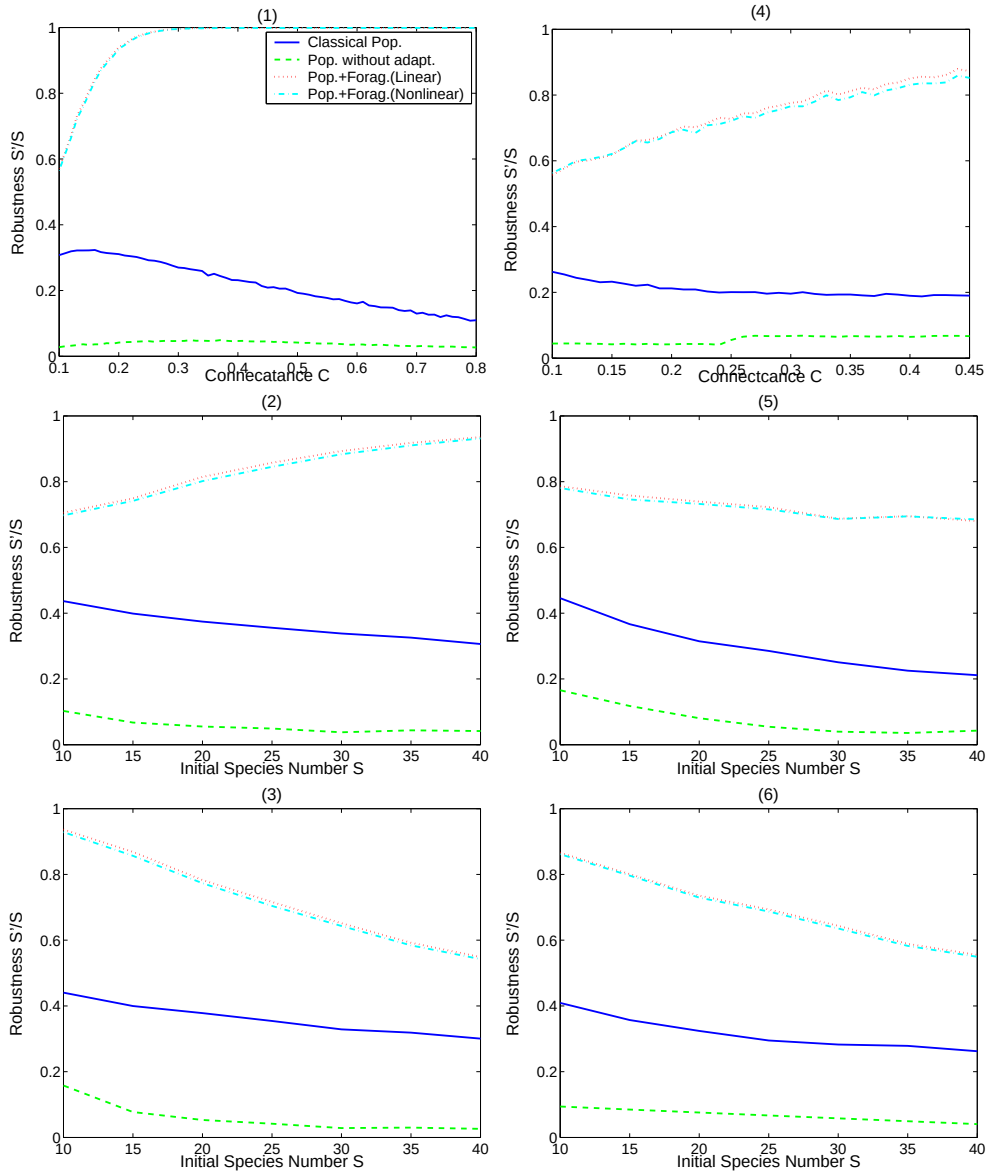


Figure 3.2: The web robustness as a function of connectance C for $S = 40$ ((1),(4)), as a function of initial species number S with connectance $C = 0.2$ fixed ((2),(5)) and with fixed connectivity $K = 4$ ((3),(6)) for random webs ((1),(2),(3)) and niche model webs ((4),(5),(6)). The four lines in each figure correspond to simulations with classical population dynamics (solid line), with population dynamics without adaptation (dashed line), with population dynamics with adaptive foraging and linear constraints (dotted line) or nonlinear constraints (dash-dotted line) on the efforts.

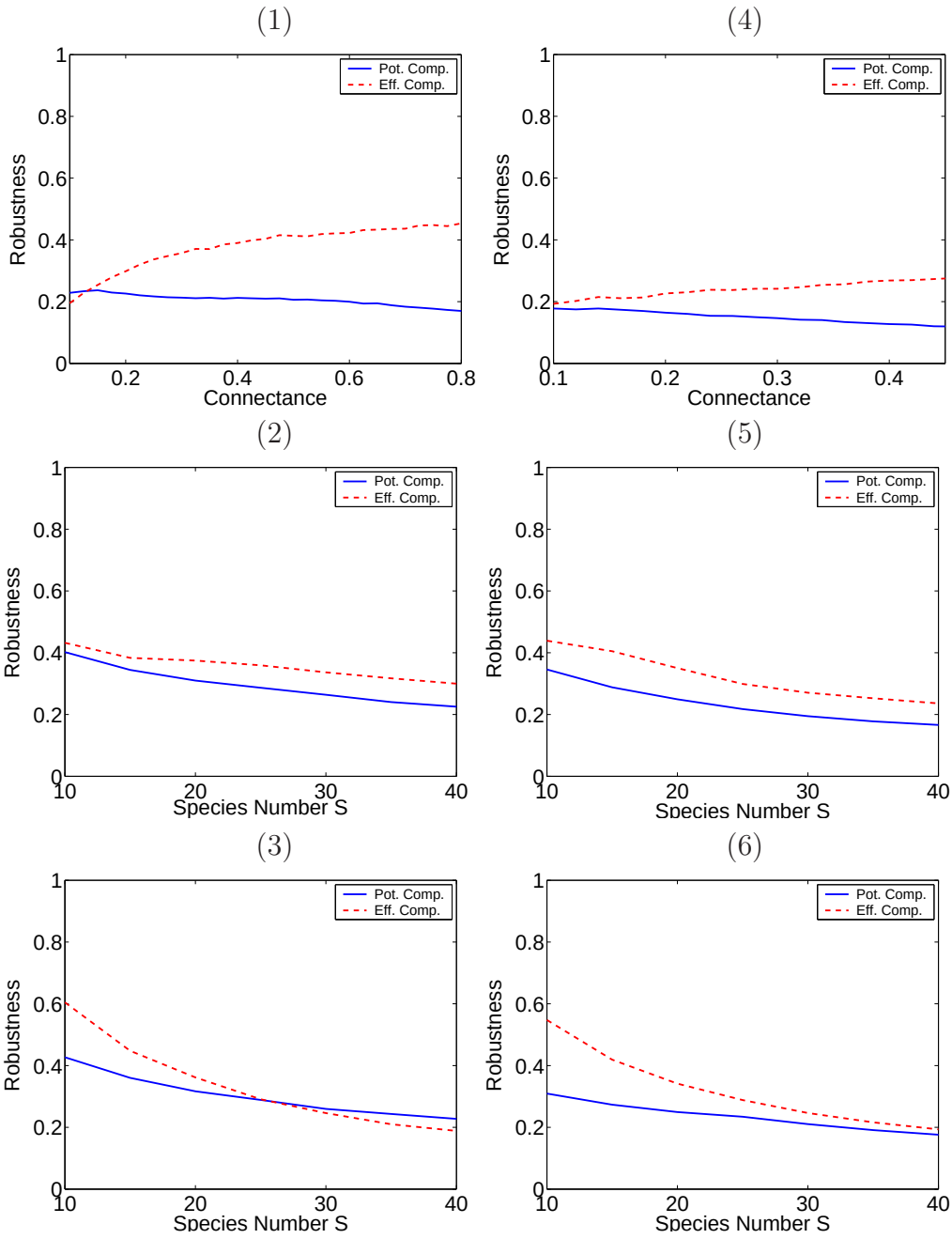


Figure 3.3: As in Figure 3.2, but with interspecific competition. The solid and dashed lines correspond to simulations with population and foraging dynamics (linear constraints), where the competition is defined by potential links and effective links.

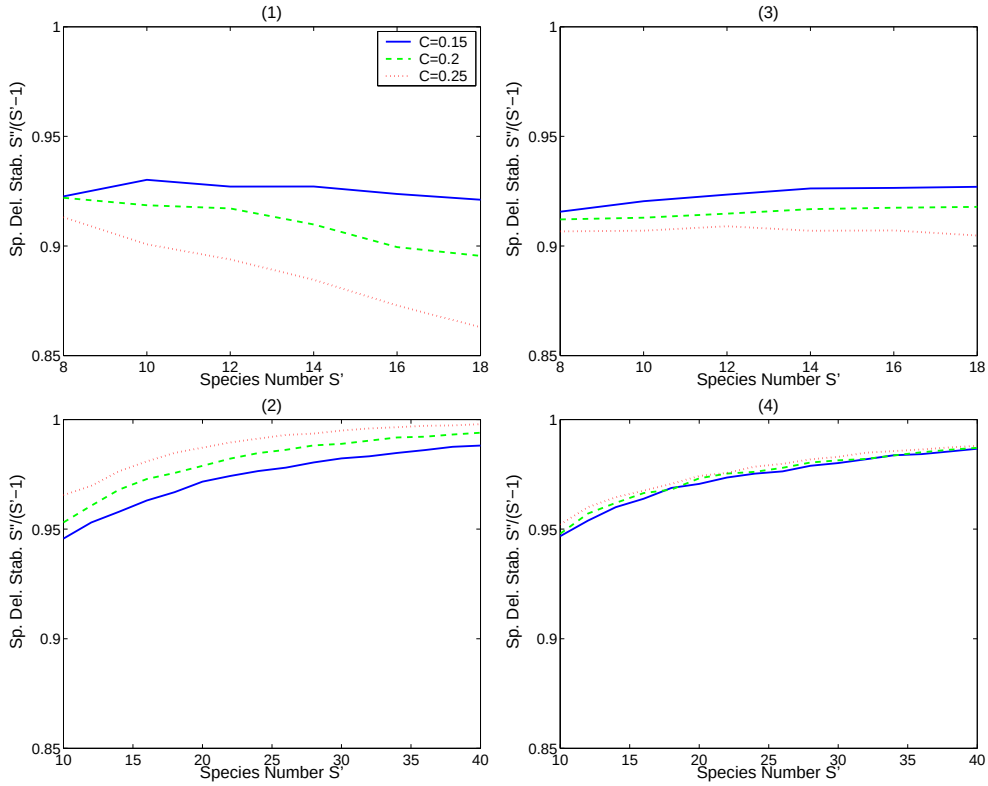


Figure 3.4: The species deletion stability for only population dynamics ((1),(3)) and population dynamics with foraging (linear constraints) ((2),(4)) as a function of S' and C. The left figures ((1),(2)) are for random webs and right ((3),(4)) for niche webs. The species deletion stability is defined as $S''/(S'-1)$, where S'' is the number of species which are alive after deletion of one species.

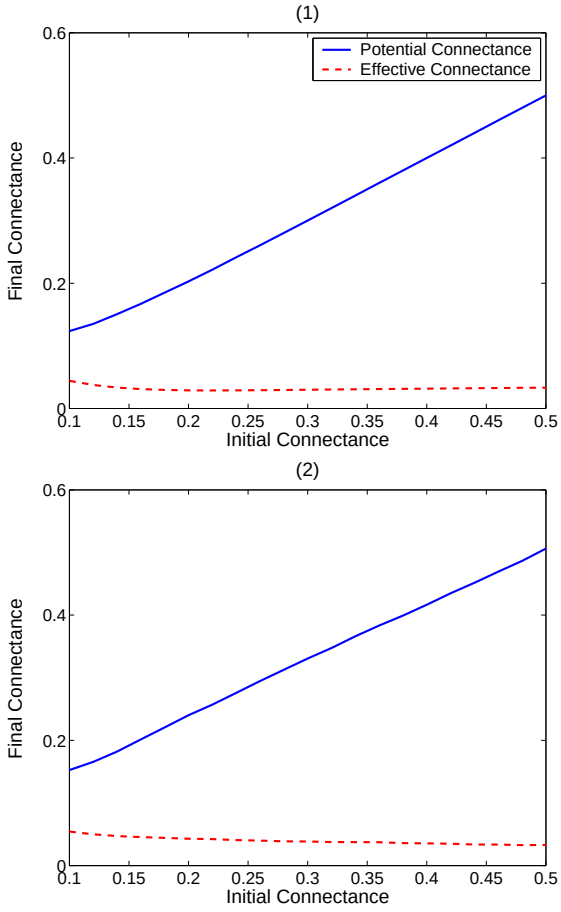


Figure 3.5: Initial connectance vs final connectance of foraging dynamics (linear) for random webs (left figures (1)) and for niche webs (right figures (2)). The vertical lines are not parameter (connectance) C but actual initial connectance of produced webs defined by $L/(S+E)S$, where L is the number of links at time $t = 0$ and $S = 40$, $E = 2$ are the initial number of species and the number of resources respectively.

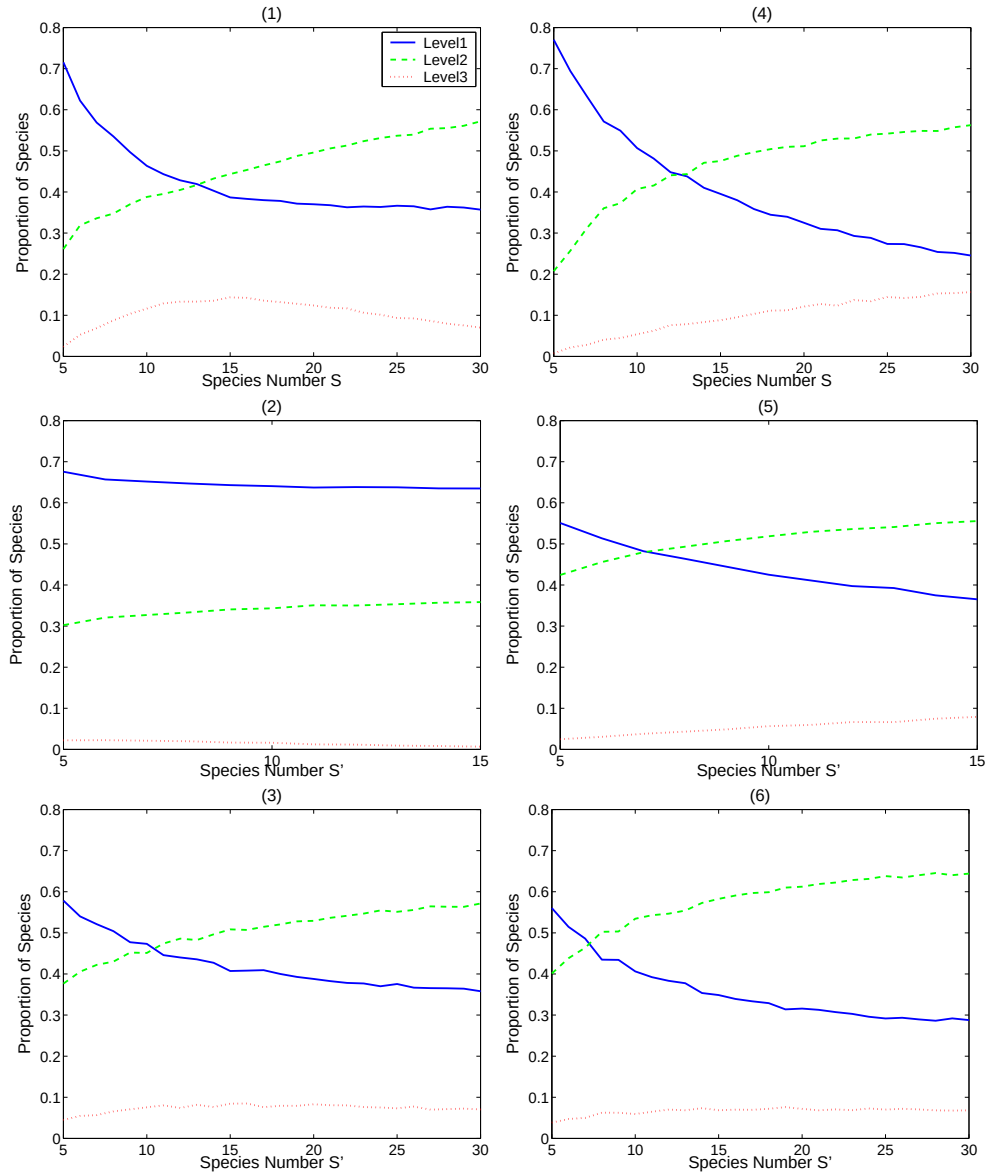


Figure 3.6: Trophic level structure of random webs ((1),(2),(3)) and niche webs ((4),(5),(6)). The top figures ((1),(4)) show the initial structures (numerically simulated), the middle ((2),(5)) the final structure of the model only with population dynamics and the bottom figures ((3),(6)) the final trophic level structure of the model with foraging (linear) dynamics calculated by the effective connection a'_{ij}. The results are similar if the structures are calculated by the potential connection a_{ij}. In all the simulations $C = 0.2$.

Chapter 4

Stability of Fixed Points

In this chapter we investigate the stability of fixed points of Lotka-Volterra systems with and without (conventional) adaptive foraging, i.e., with linear constraints. The investigated equation systems are

1. *Population dynamics without foraging dynamics*

$$\frac{dN_i(t)}{dt} = N_i(t)G_i, \tag{4.1}$$

$$G_i = \sum_{j\in B_i} \lambda_{ij}a_{ij}N_j(t) - \sum_{k\in R_i} a_{ki}N_k(t) - \beta_i N_i(t) - \alpha_i, \tag{4.2}$$

2. *Population dynamics with foraging dynamics*

$$\frac{dN_i(t)}{dt} = N_i(t)G_i, \tag{4.3}$$

$$G_i = \sum_{j\in B_i} \lambda_{ij}a_{ij}f_{ij}(t)N_j(t) - \sum_{k\in R_i} a_{ki}f_{ki}(t)N_k(t) - \beta_i N_i(t) - \alpha_i, \tag{4.4}$$

$$\frac{df_{ij}(t)}{dt} = \kappa f_{ij}(t)F_{ij}, \tag{4.5}$$

$$F_{ij} = \lambda_{ij}a_{ij}N_j(t) - \sum_{j'\in B_i} \lambda_{ij'}a_{ij'}f_{ij'}(t)N_{j'}(t). \tag{4.6}$$

We call F_{ij} the growth rate of foraging effort f_{ij}. The effects of external resources with fixed population sizes can be absorbed into the parameter α_i by redefining $\alpha_i' = \alpha_i - E_i$ with E_i being the total energy in-flow from external resources. Therefore, we assume that B_i does not include external resources in this chapter. If the energy in-flow E_i is so large that it compensates for the mortality α_i, the new parameter $\alpha_i' =: -E_i'$ takes a negative value. Therefore, we assume that α_i can take all real values. These equations include as a special case a model where basal species have logistic growth $E_i'(1-N_i/K_i)N_i$, because the maximal growth rate E_i' and carrying capacity K_i can be again included into the parameters α_i and β_i.

After an analytical investigation of local and global stability, in section 4.3 we describe a numerical study of a small food web whose topology does not satisfy the conditions found in the first two sections for local or global stability. Section 4.4 summarizes the conclusions of this chapter.

4.1 Local stability

Local stability (or linear stability) of a fixed point $\vec{x}^*$ of a dynamical system $\frac{d\vec{x}}{dt} = \vec{F}(\vec{x})$ means that any small perturbation added to the fixed point ($\vec{y} = \vec{x} - \vec{x}^*$) tends to zero. The equation governing the time evolution of perturbations is called the perturbation equation and is given by a linear equation

$$\frac{d\vec{y}}{dt} = J\vec{y}, \tag{4.7}$$

where J is the Jacobi matrix at the fixed point $\vec{x}^*$. Therefore, the structure of the Jacobi matrix determines the local stability of a fixed point.

Often the local stability of a fixed point is studied by investigating the eigenvalues of the Jacobi matrix. But we take here another approach: we look for a positive quadratic Lyapunov function $V(\vec{y}) = \sum_m C_m y_m^2$ with positive coefficients C_m, whose time derivative $\frac{dV}{dt}$ is always negative except for $\vec{y} = \vec{0}$. If we can find such a quadratic function (or equivalently find such a set of positive parameters C_m), the perturbation $\vec{y}$ tends to zero as t tends to ∞, thus the fixed point is locally stable. We remark that this Lyapunov function can be applied only near the fixed point, because it is a Lyapunov function for the perturbation equation, and the perturbation equation is a good approximation to the original nonlinear system (i.e., the Lotka-Volterra equation system) only near the fixed point (See the next section 4.2 on global stability). We also note that this is a sufficient condition for local stability, i.e., a fixed point can be locally stable even though there is no such simple quadratic form $V(\vec{y}) = \sum_m C_m y_m^2$ for the Lyapunov function (Arnold, 1998).

The time derivative of the Lyapunov function is also given by a quadratic form:

$$\begin{aligned} \frac{dV}{dt} &= \sum_m \frac{\partial V}{\partial y_m}\frac{dy_m}{dt} && (4.8)\\ &= 2\sum_m \sum_n C_m J_{mn} y_m y_n && (4.9)\\ &= \sum_m \sum_n (C_m J_{mn} + C_n J_{nm}) y_m y_n. && (4.10) \end{aligned}$$

Thus the goal is now to find a condition for the Jacobi matrix J that makes it possible to find a set of positive parameters C_m so that the quadratic form (4.10) is semi negative definite. In this section, we find a weaker topological condition than that of the original Quirk-Ruppert theorem. It will be also proved that the condition for a fixed point of population dynamics coupled to foraging dynamics is weaker than that for population dynamics only.

4.1.1 Population dynamics without adaptive foraging

We denote the set of all the species by S and the number of species by s. A fixed point P of the Lotka-Volterra equation system (4.1) is then denoted by $(n_1, n_2, \cdots, n_s)$. Since $N_i = 0$ or $G_i = 0$ implies $dN_i/dt = 0$ (and vice versa) and,

except for very special cases, the solution n_i of the equation $G_i = 0$ is nonzero, there are in general 2^s fixed points in phase space: $(n_1 = 0, n_2 = 0, \cdots, n_s = 0), (n_1 \neq 0, n_2 = 0, \cdots, n_s = 0), \cdots, (n_1 \neq 0, n_2 \neq 0, \cdots, n_s \neq 0)$. Because the equation system for non-zero n_i $(1 \leq i \leq s)$ is just a linear equation system, n_i can formally take a positive or a negative value. That is, there is no mathematical reason why n_i should be non-negative. Of course only the solutions having non-negative values are biologically meaningful. Any system has at least one fixed point where all the population sizes are non-negative: $(n_1 = 0, n_2 = 0, \cdots, n_s = 0)$. If we assume that there is at least one species whose total amount of energy in-flow from external resources is larger than mortality (i.e., $E_i' > 0$), then there is at least one fixed point with non-negative values different from the origin. The goal of this subsection is to find a weaker topological condition than the condition of the Quirk-Ruppert theorem under which a fixed point is linearly stable.

For $i \in S$, the set of links from its prey is denoted by L_i (i.e., $L_i = \{(i,j)|j \in B_i\}$). Then $L = \cup_{i \in S} L_i$ is the set of all the links in a food web. It can be assumed that L does not include a self-loop (i,i) without loss of generality, because the effect of a self loop can be included into the competition term if we define $\beta_i' = \beta_i + (1 - \lambda_{ii})a_{ii}$. At a fixed point P, we divide the s species into two categories: $S = \overline{S} \cup \underline{S}$, where $\overline{S} = \{i|n_i \neq 0\}$ and $\underline{S} = \{i|n_i = 0\}$. For example, the zero fixed point $(0, 0, \cdots, 0)$ corresponds to $(\overline{S} = \emptyset, \underline{S} = S)$. We call species in $\overline{S}$ "living" species (even if n_i can take a negative value) and species in $\underline{S}$ extinct species. Corresponding to this, we define a set of "living" links by $\overline{L} = \{(i,j)|i \in \overline{S}, j \in \overline{B_i}\}$, where $\overline{B_i}$ is the set of living prey of i. That is, $\overline{L}$ is the set of links between all the "living" species.

We call $\overline{S}$ a "living" pattern (this gives us information about which species are "living") and a 2-tuple $(\overline{S}, \overline{L})$ a configuration (this is a food web constructed by only "living" species $\overline{S}$). We notice that each fixed point corresponds to one "living" pattern and to one configuration, because specifying a fixed point uniquely determines the sets $\overline{S}$ and $\overline{L}$. If the fixed point corresponding to some "living" pattern and configuration is stable, the "living" pattern and the configuration are called stable.

Now we consider the quadratic form $dV/dt = \sum_{i \in S} \sum_{n \in S} A_{in} := W(\vec{y})$, where $A_{in} = (J_{in}C_i + J_{ni}C_n)y_i y_n$ and J_{in} is the $(i,n)-$element of the Jacobi matrix at a fixed point P. J_{in} takes a non-zero value for "living" species $i \in \overline{S}$ only if species n is either a prey, a predator or i itself. If i is extinct at fixed point P, J_{in} takes a non-zero value only if n is i itself. The eigenvalues of Jacobi matrix J for all the possible cases are written in Tables 4.1 and 4.2.

We notice that it could happen that a species j is both a prey and a predator of species i. In this case, the value of the Jacobi matrix is obtained by adding $n_i \lambda_{ij} a_{ij} + (-n_i a_{ji})$. From Tables 4.1 and 4.2, we immediately find the necessary conditions for "living" species and extinct species.

- *Necessary condition for species (nodes)*

  (p-1) The population size of any "living" species $(i \in \overline{S})$ is positive at the fixed point: $n_i > 0$. The species i is called a surviving species. We notice

n	J_{in}
$j \in B_i$	$n_i \lambda_{ij} a_{ij}$
$k \in R_i$	$-n_i a_{ki}$
$j \in R_i \cap B_i$	$n_i \lambda_{ij} a_{ij} - n_i a_{ji}$
i	$-\beta_i n_i$
otherwise	0

Table 4.1: $J_{in} (i \in \overline{S})$

n	J_{in}
i	G_i
otherwise	0

Table 4.2: $J_{in} (i \in \underline{S})$

that the growth rate of a surviving species at the fixed point is zero: $G_i = 0$.

(p-2) The growth rate of any extinct species $i \in \underline{S}$ is negative at the fixed point: $G_i < 0$. In this case, $n_i = 0$. This means that the total energy inflow from prey can not compensate for the total energy loss by predation, self competition and mortality at the fixed point: $\sum_{j \in B_i} \lambda_{ij} a_{ij} n_j < \sum_{k \in R_i} a_{ki} n_k + \beta_i n_i + \alpha_i$.

Both conditions (p-1) and (p-2) are necessary in order that the fixed point P is linearly stable (or the quadratic form (4.10) is semi negative definite). The necessity of (p-1) can be understood by considering the perturbation equation $dy_i/dt = J_{ii} y_i$ with the initial condition $y_i(0) \neq 0, y_n(0) = 0$ $(n \neq i)$. If n_i is negative, the perturbation y_i grows because $J_{ii} = -\beta_i n_i$ is positive. Therefore, the fixed point P is unstable for such perturbations. Condition (p-2) is also necessary because of the perturbation equation $dy_i/dt = G_i y_i$ (in this case, the initial condition can be arbitrary). If the growth rate at the fixed point were positive (i.e., if the condition (p-2) were broken), y_i would not vanish but grow. Conversely, if (p-2) is satisfied, y_i always approaches zero regardless of perturbations to other species, thus all the perturbations to extinct species become negligible in sufficiently large time t. This indicates that extinct species do not contribute to the stability of the fixed point P (for example, it does not matter what topology extinct species have) so long as (p-2) is satisfied. Therefore, in this case, only the surviving species are important for stability. These conditions can be restated as a condition on the pair (n_i, G_i): the point (n_i, G_i) in the $x-y$ plane has to be placed on the positive part of the $x-$axis or the negative part of the $y-$axis. This will become important when considering global stability (section 4.2). From now onward, we assume that conditions (p-1) and (p-2) are satisfied at a fixed point P and call $\overline{S}$ a surviving pattern.

Now we perform calculation of the quadratic form $dV/dt = \sum_{i \in S} \sum_{n \in S} A_{in} := W(\vec{y})$ with $A_{in} = (J_{in} C_i + J_{ni} C_n) y_i y_n$, taking the Jacobi matrix into account. We

decompose the quadratic form:

$$W(\vec{y}) = \sum_{i\in S}\sum_{n\in S} A_{in} \tag{4.11}$$

$$= \sum_{i\in S}(\sum_{j\in B_i} A_{ij} + \sum_{k\in R_i} A_{ik} + A_{ii}) \tag{4.12}$$

$$= 2\sum_{i\in S}\sum_{j\in B_i} A_{ij} + \sum_{i\in S} A_{ii}. \tag{4.13}$$

The last equality comes from the fact that both $\sum_{i\in S}\sum_{j\in B_i}$ and $\sum_{i\in S}\sum_{k\in R_i}$ are the sum over all the links in the food web, thus $\sum_{i\in S}\sum_{k\in R_i} A_{ik} = \sum_{k\in S}\sum_{i\in B_k} A_{ik}$, and if we replace (i,k) by (j,i) for the last summation, we get $\sum_{i\in S}\sum_{j\in B_i} A_{ji}$, and further because of the symmetry of A_{ij}, we obtain at last $\sum_{i\in S}\sum_{j\in B_i} A_{ij}$.

What we need to do now is to find a condition to determine positive parameters C_i such that the first term in (4.13) vanishes and the second term is negative. First, we deal with the first term:

$$\sum_{i\in S}\sum_{j\in B_i} A_{ij} = \sum_{i\in \overline{S}}\sum_{j\in \overline{B}_i} A_{ij} + \sum_{i\in \overline{S}}\sum_{j\in \underline{B}_i} A_{ij} + \sum_{i\in \underline{S}}\sum_{j\in \overline{B}_i} A_{ij} + \sum_{i\in \underline{S}}\sum_{j\in \underline{B}_i} A_{ij}. \tag{4.14}$$

Because the perturbation y_i goes to zero for an extinct species $i \in \underline{S}$, the contributions of the second, third and fourth terms become smaller and smaller with time. Therefore, we have to deal only with the first term. Substituting the eigenvalues of the Jacobi matrix J into A_{ij}, we find

$$A_{ij} = (J_{ij}C_i + J_{ji}C_j)y_iy_j \tag{4.15}$$

$$= a_{ij}(C_in_i\lambda_{ij} - C_jn_j)y_iy_j. \tag{4.16}$$

Since the perturbations y_i, y_j are arbitrary, in order that A_{ij} vanish, the quantity $C_in_i\lambda_{ij} - C_jn_j$ has to vanish for $\forall i \in \overline{S}$ and $\forall j \in \overline{B_i}$. In other words, the equation system $C_in_i\lambda_{ij} - C_jn_j = 0$ must have a positive solution C_i. (Because the equation is linear homogeneous and all the parameters λ_{ij}, n_i, n_j are positive, this condition is equivalent to the condition "the equation system has a solution".) This equation system can be simplified by a transformation of the variable $p_i := C_in_i$ to the equation system $p_i\lambda_{ij} - p_j = 0$ for p_i, p_j.

If j is both a prey and a predator of i, $J_{ij} = n_i\lambda_{ij}a_{ij} - n_ia_{ji}$ and $J_{ji} = n_j\lambda_{ji}a_{ji} - n_ja_{ij}$. Then

$$A_{ij} = (J_{ij}C_i + J_{ji}C_j)y_iy_j \tag{4.17}$$

$$= a_{ij}(C_in_i\lambda_{ij} - C_jn_j)y_iy_j + a_{ji}(C_jn_j\lambda_{ji} - C_in_i)y_iy_j. \tag{4.18}$$

In order that this term should vanish, two equations must be satisfied: $C_in_i\lambda_{ij} - C_jn_j = 0$ and $C_in_i\lambda_{ij} - C_jn_j = 0$. The first equation appeared because j is a prey of i and the second because i is a prey of j.

With these parameter values, together with the value of the Jacobi matrix $J_{ii} = -\beta_in_i$, the term $A_{ii} = 2J_{ii}C_iy_i^2$ turns out to be always negative except for the case $y_i = 0$ $(\forall i)$. Therefore for sufficiently large time t, $dV/dt = W(\vec{y})$ is negative, thus we find that the fixed point is linearly stable.

We can say that the condition $p_i\lambda_{ij} - p_j = 0$ applies to the topology of webs because we obtain one equation (or one constraint for the parameter p_i) for each connected pair of species. Therefore the topology of a web is reflected in the structure of the system of equations $\lambda_{ij}p_i = p_j$. For example, if all the species are connected with randomly chosen energy conversion efficiency λ_{ij}, we have $s(s-1)$ links, therefore $s(s-1)$ equations for s parameters. In this case, the equation system is not solvable. Thus a food web with the above topology can not satisfy the condition $p_i\lambda_{ij} - p_j = 0$ for all $i \in S$ and $j \in B_i$.

So we have found a sufficient condition for the links.

- *Sufficient condition for the links (edges)*

  (p-3) For each link (i, j) between surviving species in $\overline{L}$ (note: not L), we get an equation $p_i\lambda_{ij} = p_j$. This coupled system of equations has a positive solution.

The condition can be seen also as a condition for energy conversion efficiency λ_{ij}:

$$\exists(p_1 > 0, p_2 > 0, \cdots, p_s > 0),\ \forall i \in S,\ \forall j \in B_i,\ [\lambda_{ij} = p_j/p_i], \tag{4.19}$$

which states that energy conversion efficiency λ_{ij} can be written as the ratio between parameters p_i and p_j for all pairs of predator and prey. Because a condition of this form will appear often in the subsequent sections, we wrote the condition in a general form and we refer to this condition as Condition I from now on. In order that a fixed point of the population dynamics without adaptive foraging is stable, the topology of the total web (S, L) does not have to satisfy this condition but the surviving web $(\overline{S}, \overline{L})$ must satisfy this condition.

Whether or not a web satisfies Condition I depends only on the topology of the web and does not depend on the parameter values of the system (e.g., connection strength or the strength of intraspecific competition). Some examples of food webs that satisfy Condition I are displayed in Figure 4.1. Example (a) is a topology with a tree structure which satisfies the condition of the Quirk-Ruppert theorem. A food web with topology (b) is constructed in layers and does not have any omnivore. This type of topology is used in the next chapter, where stability under evolution is investigated. Example (c) is a topology where there are very special omnivores. In (d), the web has perfect conversion efficiency $\lambda_{ij} = 1$.

4.1.2 Population dynamics with adaptive foraging

In the previous subsection, we found a topological condition for the linear stability of a fixed point P. The condition is much weaker than the topological condition offered by the Quirk-Ruppert theorem due to the special properties of the Lotka-Volterra equation system without adaptive foraging. Now the question is what happens if we couple the population dynamics with foraging dynamics. A difficulty is that we have to consider two different types of dynamics at once: population dynamics for species and foraging dynamics for links, and we have to consider the

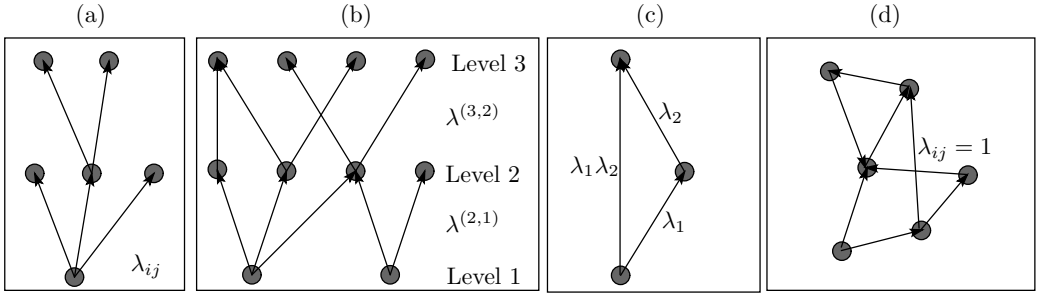


Figure 4.1: Four examples of the condition (4.19).

stability of a fixed point P of the coupled system. (Note: Here P is not the fixed point of population dynamics only, but of the coupled system.)

One important feature of foraging dynamics concerning the topology of food webs is that the potential link structure defined by the non-zero values of a_{ij} and the effective link structure defined by the non-zero values of $a_{ij}f_{ij}$ are different, i.e., the foraging dynamics strongly affects the effective topology of webs. This occurs because some foraging efforts f_{ij} go to zero (see chapter 2 and chapter 3).

In this subsection, therefore, we divide the link set L into two categories containing the information about effective link structure: $L^{(1)}$ and $L^{(2)}$, where $L^{(1)} = \{(i,j)|f^*_{ij} \neq 0\}$ and $L^{(2)} = \{(i,j)|f^*_{ij} = 0\}$ ($*$ denotes the value at the fixed point). That is, $L^{(1)}$ is the set of links whose foraging efforts at the fixed point are nonzero, and it is called the effective link structure (or the set of activated links). In this sense, we call L the potential link structure.

On the other hand, we divide the species set S and the link set L into two categories as was done in the previous subsection according to the surviving pattern: $S = \overline{S} \cup \underline{S}$ and $L = \overline{L} \cup \underline{L}$. Combining these two classifications, we also use notation such as $\overline{L}^{(1)} = \overline{L} \cap L^{(1)}$ (effective links spanned by surviving species). And we call the pair $(\overline{S}, \overline{L}^{(1)})$ an effective configuration. Clearly one effective configuration corresponds to one fixed point.

Concerning extinct species, we saw in the previous subsection from the discussion of condition (p-2) that an extinct species does not contribute to the stability of a fixed point if (p-2) is satisfied at the fixed point. The reason for this was that the perturbation equation for the extinct species depends only on its own growth rate. The mechanism behind this can be understood if we observe the original equation $dN_i/dt = N_iG_i$ for extinct species. The point is that the right hand side is the product of the variable N_i and the function G_i. Due to this form, all the values of Jacobi matrix J_{in} at a fixed point $n_i = 0$ vanish except for the case of $n = i$.

We also notice that the form of the foraging dynamics is similar, $df_{ij}/dt = \kappa f_{ij}F_{ij}$. This implies that all zero foraging efforts $f_{ij} = 0$ do not contribute to the stability of fixed points. Thus, only the effective link structure is important.

In spite of these differences, this system must reflect the properties of a system that has population dynamics only. Therefore, we expect similar conditions for the stability of fixed points. That is to say, we expect that a fixed point P of

the coupled dynamics with effective configuration $(\overline{S}, \overline{L}^{(1)})$ is linearly stable if the following conditions are satisfied

- *Necessary condition for the species (nodes)*

  (f-1) The population size of any "living" species ($i \in \overline{S}$) at the fixed point is positive: $n_i > 0$.
  (f-2) The growth rate of any species $i \in \underline{S}$ is negative at the fixed point: $G_i < 0$.

- *Condition for the foraging efforts (links)*

  (f-3) The foraging effort of any effective "living" link ($(i,j) \in \overline{L}^{(1)}$) is positive: $f^*_{ij} > 0$.
  (f-4) The growth rate of an inactivated link $(i,j) \in \overline{L}^{(2)}$ at the fixed point is negative: $F_{ij} < 0$. This means that the potential energy-flow from prey to predator via an inactivated link is smaller than the average energy-flow to the predator:

$$\lambda_{ij} a_{ij} n_j < \sum_{j' \in B_i} \lambda_{ij'} a_{ij'} f^*_{ij'} n_{j'}. \tag{4.20}$$

- *Sufficient condition for link structure (topology)*

  (f-5) For the effective link structure spanned by surviving species $\overline{L}^{(1)}$ (note: not L or $\overline{L}$), the equation system $\lambda_{ij} p_j = p_i$ has a positive solution.

In this subsection, we prove this proposition. But before going to the proof, we make a few comments.

For convenience, we call $\mathrm{P}^p(n_1, n_2, \cdots, n_s)$ (here n_i can be zero) a fixed point of the population dynamics and $\mathrm{P}^f(\vec{f}^*_1, \vec{f}^*_2, \cdots, \vec{f}^*_s)$ a fixed point of the foraging dynamics, and we drop the symbol $*$ for the indication of a fixed point. We notice that $\mathrm{P} = \mathrm{P}^p \times \mathrm{P}^f$.

In contrast to the system with population dynamics only (the previous subsection), there may be many fixed points corresponding to a surviving pattern $\overline{S}$, because it is possible that two different fixed points have the same surviving patterns but different effective connections. The number of such fixed points is equal to the number of possible effective link structures (or the number of configurations with a fixed surviving pattern). Therefore, in order for a surviving pattern $\overline{S}$ to be stable, it is enough that there exists only one fixed point that satisfies the conditions (f-1)-(f-5). This is the main difference between population dynamics with and without foraging dynamics. For example, we consider the full surviving pattern $\overline{S} = S$ where all the species are surviving. For population dynamics without adaptive foraging, only one fixed point is related to the pattern. Therefore, this fixed point has to be stable in order that the surviving pattern is stable. But, for population dynamics with foraging dynamics, many fixed points correspond to the

surviving pattern. And we have more and more fixed points as the connectance increases because we have more possibilities for effective link structures.

One further property of foraging dynamics is that each surviving pattern $\overline{S}$ has at least one fixed point whose effective link structure satisfies condition (f-5). Link structures where each surviving species has only one effective prey (i.e., $\forall i \exists j f_{ij} = 1$) and where there is at least one species that feeds on an external resource are an example. In this case, there are at most $\overline{s}-1$ links (thus equations) for $\overline{s}$ variables. (Recall that B_i does not include external resources. Therefore links to external resources are not counted.) This equation system has a solution. For such configurations, only conditions (f-1)-(f-4) must be considered to determine if the surviving pattern $\overline{S}$ is stable. Most importantly, a food web obtains more link structures that satisfy condition (f-5) as the average number of prey per species increases. For example, if each species has K prey, there are K^s link structures where each species has only one effective prey. If we apply this argument to the full surviving pattern $\overline{S} = S$, we expect that there will be more ways to obtain a stable surviving pattern $\overline{S} = S$ as the average number of prey per species K increases (and thus as connectance increases).

Now we turn to the proof of the proposition. We take a fixed point P with effective configuration $(\overline{S}, \overline{L}^{(1)})$ that satisfies conditions (f-1)–(f-5). First we mention three properties of the equation system for use in the following calculations:

1. We always set the initial efforts $f_{ij}(0)$ so that their sum over prey is 1. Then for all time t, the efforts $f_{ij}(t)$ sum up to 1 (chapter 2):

$$\sum_{j \in B_i} f_{ij}(0) = 1 \Rightarrow \sum_{j \in B_i} f_{ij}(t) = 1 \ (\forall t). \tag{4.21}$$

2. At a fixed point, the potential energy in-flow to a predator from its prey ($I_{ij} = \lambda_{ij} a_{ij} n_j$) through an activated link $(i,j) \in L^{(1)}$ is the same for all prey. That is,

$$I_{ij} = I_{ij'} \ (j, j' \in B_i^{(1)}) \tag{4.22}$$

must hold for i and $j, j' \in B_i^{(1)}$. We therefore drop the index j and denote the potential energy in-flow to species i by I_i.

This potential energy flow is equal to the average energy flow at the fixed point:

$$I_i = \sum_{j' \in B_i} \lambda_{ij'} a_{ij'} f^*_{ij'} n_j. \tag{4.23}$$

Therefore condition (f-4) can be restated as "The potential energy in-flow through an inactivated link $(i,j) \in L^{(2)}$ is smaller than I_i".

3. If B_i (and therefore R_i) contains i, $f_{ii}(t)$ always approaches zero, because the growth rate of such foraging effort is negative. That is, even if there is a potential self-loop, the effective self-loop always disappears. Therefore, we assume from now on that B_i (and R_i) do not contain i.

Because we have to deal with the population dynamics and foraging dynamics at once, we write the equation system using a combined vector $\vec{x} = (N_1, \vec{f_1}, \cdots, N_s, \vec{f_s})$,

$$\frac{d\vec{x}}{dt} = \vec{D}(\vec{x}), \tag{4.24}$$

and denote the m-th component of $\vec{x}$ by x_m, where m is a member of the set $S \cup L$. In the following calculation, we use notation such as $m = i \in S$ (m is species i) or $m = l_i = (i, j) \in L_i$ (m is link $l_i = (i, j)$, i.e., the link from prey j to i). The perturbation equation at the fixed point($y_m = x_m - x_m^*$) is then given by

$$\frac{d\vec{y}}{dt} = J\vec{y}, \tag{4.25}$$

where J is the Jacobi matrix of the system at the fixed point P. The Jacobi matrix for this system is given in Tables 4.3-4.6.

n	J_{in}
$j \in B_i$	$n_i \lambda_{ij} a_{ij} f_{ij}$
$k \in R_i$	$-n_i a_{ki} f_{ki}$
i	$-\beta_i n_i$
$(i, j) \in L_i$	$\lambda_{ij} a_{ij} n_i n_j$
$(k, i) \in L_k (k \in R_i)$	$-a_{ki} n_i n_k$
otherwise	0

Table 4.3: $J_{in} (i \in \overline{S})$

n	J_{in}
i	G_i
otherwise	0

Table 4.4: $J_{in} (i \in \underline{S})$

n	$J_{l_i n}$
$j \in B_i$	$\kappa f_{ij} \lambda_{ij} a_{ij} - \kappa f_{ij}^2 \lambda_{ij} a_{ij}$
$j' (\neq j) \in B_i$	$-\kappa f_{ij} \lambda_{ij} a_{ij} f_{ij'}$
$l_i' = (i, j') \in L_i$	$-\kappa f_{ij} \lambda_{ij'} a_{ij'} n_{j'}$
otherwise	0

Table 4.5: $J_{l_i n} (l_i = (i, j) \in L_i^{(1)})$

n	$J_{l_i n}$
l_i	$\kappa(\lambda_{ij} a_{ij} n_j - I_i)$
otherwise	0

Table 4.6: $J_{l_i n} (l_i = (i, j) \in L_i^{(2)})$

We also use the following properties of the perturbations for foraging dynamics:

1. Due to property 1 of the foraging dynamics (Equation (4.21)), the quantity $\sum_{j\in B_i} y_{ij}$ must vanish for all times, because of the definition of y_{ij}. Because all the variables x_m have to be positive, the perturbation must be positive for an inactivated link $(i,j) \in L^{(2)}$: $y_{ij} > 0$. Therefore, taking into account $\sum_{j\in B_i} y_{ij} = \sum_{j\in B_i^{(1)}} y_{ij} + \sum_{j\in B_i^{(1)}} y_{ij}$, the sum of perturbations added to activated links is negative: $\sum_{j\in B_i^{(1)}} y_{ij} = -\sum_{j\in B_i^{(1)}} y_{ij} < 0$.

2. Because of the values of the Jacobi matrix, the perturbations to inactivated links vanish: $y_{ij} \to 0$ for inactivated links $(i,j) \in L^{(2)}$. This implies that the sum of the perturbations of activated links vanishes: $\sum_{j\in B_i^{(1)}} y_{ij} \to 0$ for activated links. This does not yet mean that the perturbation for each activated foraging effort vanishes. We will, therefore, prove in the following that the perturbation for each foraging effort tends to vanish: $y_{ij} \to 0$ ($\forall i \in S \forall j \in B_i$).

To show that the fixed point P is stable, we take the same route as we did for population dynamics only in the previous subsection. We try to zero all the terms in the quadratic form $dV/dt = \sum_{m\in S\cup L}\sum_{n\in S\cup L} A_{mn} := W(\vec{y})$, where $A_{mn} = (C_m J_{mn} + C_n J_{nm}) y_m y_n = A_{nm}$ except for the square terms A_{mm}, and this will be done by showing that it is possible to find positive coefficients C_m that make the quadratic form $W(\vec{y})$ semi-negative definite. Decomposing the sum of the quadratic form $W(\vec{y})$ as

$$\sum_{m\in S\cup L}\sum_{n\in S\cup L} A_{mn} = \underbrace{\sum_{m\in S}\sum_{n\in S} A_{mn}}_{\text{part I}} + \underbrace{\sum_{m\in L}\sum_{n\in L} A_{mn}}_{\text{part II}} + 2\underbrace{\sum_{m\in L}\sum_{n\in S} A_{mn}}_{\text{part III}}, \tag{4.26}$$

we deal with the interactions between population dynamics-population dynamics (part I), foraging dynamics-foraging dynamics (part II) and foraging dynamics-population dynamics (part III) independently. Here we mention that, through the calculation, we will find that the foraging dynamics does not contribute to the negativeness of the quadratic form, i.e., only the self competition terms $A_{ii} = 2J_{ii}C_i y_i^2 = -2\beta_i n_i C_i y_i^2$ for $i \in S$ contribute to the negativeness.

Part I: population dynamics-population dynamics

This part was also covered in the previous subsection about population dynamics without adaptive foraging. Exactly as was done there, decomposing this part into two terms according to whether a species is surviving ($\overline{S}$) or extinct ($\underline{S}$), we find that only if $J_{ij}C_i + J_{ji}C_j$ vanishes, for all $i \in \overline{S}$ and $j \in \overline{B}_i$ with positive parameter C_i, does the term $\sum_{m\in S}\sum_{n\in S} A_{mn}$ becomes negative. Taking into account the elements of the Jacobi matrix, we get

$$J_{ij}C_i + J_{ji}C_j = a_{ij}f_{ij}(C_i n_i \lambda_{ij} - C_j n_j). \tag{4.27}$$

Here we find a difference to last subsection: this term is proportional to the effective connection strength $a_{ij}f_{ij}$. Because the foraging effort for inactivated link is zero

($f_{ij} = 0$ for $j \in \overline{B}_i^{(2)}$), this term automatically vanishes for inactivated links. Therefore, what we need is to satisfy the equation

$$C_i n_i \lambda_{ij} - C_j n_j = 0, \tag{4.28}$$

only for $i \in \overline{S}$ and $j \in \overline{B}_i^{(1)}$ (or activated links $(i,j) \in \overline{L}^{(1)}$). Of course this equation system has solutions because of condition (f-5). And because the coefficients C_i are positive, the square term

$$A_{ii} = 2J_{ii}C_i y_i^2 = -2\beta_i n_i C_i y_i^2 \tag{4.29}$$

is negative for all $i \in \overline{S}$ except for the point $y_i = 0$.

Part II: foraging dynamics-foraging dynamics

The second part can be written as

$$\sum_{m\in L}\sum_{n\in L} A_{mn} = 2\sum_{m\in L}\sum_{n\in L} J_{mn}C_m y_m y_n. \tag{4.30}$$

Taking into account the elements of the Jacobi matrix, the summation can be simplified to

$$\sum_{m\in L}\sum_{n\in L} = \sum_{i\in S}\sum_{i'\in S}\sum_{l_i\in L_i}\sum_{l_{i'}\in L_{i'}} \tag{4.31}$$

$$= \sum_{i\in S}\sum_{l_i\in L_i}\sum_{l_i'\in L_i}, \tag{4.32}$$

where the second equality is obtained because the foraging dynamics of species i does not include the foraging efforts of a different species i'. The last summation can be decomposed further according to the interactions between different types of link: activated links-activated links; activated links-inactivated links; and inactivated links-activated links and inactivated links-inactivated links.

$$\sum_{l_i\in L_i}\sum_{l_i'\in L_i} = \underbrace{\sum_{l_i\in L_i^{(1)}}\sum_{l_i'\in L_i^{(1)}}}_{\text{II-(1)}} + \underbrace{\sum_{l_i\in L_i^{(1)}}\sum_{l_i'\in L_i^{(2)}}}_{\text{II-(2)}} + \underbrace{\sum_{l_i\in L_i^{(2)}}\sum_{l_i'\in L_i^{(1)}}}_{\text{II-(3)}} + \underbrace{\sum_{l_i\in L_i^{(2)}}\sum_{l_i'\in L_i^{(2)}}}_{\text{II-(4)}}. \tag{4.33}$$

The terms II-(2) and II-(3) cannot be combined because the summands are not symmetric. We remark that a summation over all the links L_i ($\sum_{l_i\in L_i}$) can be replaced by the summation over all the prey B_i ($\sum_{j\in B_i}$), because both summations have ultimately the same effect. Therefore, equation (4.33) can be written as

$$\sum_{j\in B_i}\sum_{j'\in B_i} = \underbrace{\sum_{j\in B_i^{(1)}}\sum_{j'\in B_i^{(1)}}}_{\text{II-(1)}} + \underbrace{\sum_{j\in B_i^{(1)}}\sum_{j'\in B_i^{(2)}}}_{\text{II-(2)}} + \underbrace{\sum_{j\in B_i^{(2)}}\sum_{j'\in B_i^{(1)}}}_{\text{II-(3)}} + \underbrace{\sum_{j\in B_i^{(2)}}\sum_{j'\in B_i^{(2)}}}_{\text{II-(4)}}. \tag{4.34}$$

We will treat each of these terms separately.

II-(1): activated link - activated link Because the potential energy in-flow through each activated link is the same (property 2 of the foraging dynamics), these elements of the Jacobi matrix simplify to

$$J_{(i,j),(i,j')} = -\kappa f_{ij}\lambda_{ij'}a_{ij'}n_{j'} = -\kappa f_{ij}I_i. \tag{4.35}$$

Because this is independent of prey j', we can write the double summation as the product of two summations $\sum_{j\in B_i^{(1)}}$ and $\sum_{j'\in B_i^{(1)}} y_{ij'}$:

$$\text{II-(1)} = -\kappa I_i \sum_{j\in B_i^{(1)}} f_{ij}C_{ij}y_{ij} \sum_{j'\in B_i^{(1)}} y_{ij'} \tag{4.36}$$

Now considering the fact that $\sum_{j\in B_i^{(1)}} = \sum_{j'\in B_i^{(1)}}$ and that we have free parameters C_{ij}, we set the coefficients C_{ij} for activated links $(i,j)\in L^{(1)}$ so that the value of f_{ij} is cancelled. In order to do so, we take, for example, $C_{ij} = \frac{n_i^2 C_i}{\kappa f_{ij}} > 0$. (Why we make this choice will become clear in the following.) Thus we find

$$\text{II-(1)} = -I_i n_i^2 C_i \sum_{j\in B_i^{(1)}} y_{ij} \sum_{j'\in B_i^{(1)}} y_{ij'} \tag{4.37}$$

which is, indeed, negative.

II-(2): activated link - inactivated link The form of the Jacobi matrix is similar to that of II-(1), activated link - activated link. The difference is that the potential energy in-flow through inactivated links is smaller than I_i (condition (f-4) and property 2 of the foraging dynamics). The element of the Jacobi matrix is

$$J_{(i,j),(i,j')} = -\kappa f_{ij}\lambda_{ij'}a_{ij'}n_{j'}. \tag{4.38}$$

Then the double summation with $C_{ij} = \frac{n_i^2 C_i}{\kappa f_{ij}} > 0$ is

$$\text{II-(2)} = -n_i^2 C_i \sum_{j\in B_i^{(1)}} y_{ij} \sum_{j'\in B_i^{(2)}} \lambda_{ij'}a_{ij'}n_{j'}y_{ij'}. \tag{4.39}$$

Recalling the equality $\sum_{j\in B_i^{(1)}} y_{ij} + \sum_{j\in B_i^{(2)}} y_{ij} = 0$ and the positiveness of the perturbations for inactivated links $y_{ij} > 0$ for $(i,j)\in L_i^{(2)}$ (property 1 of the perturbation equation), we obtain a negative value for the sum of the perturbations of activated links $\sum_{j\in B_i^{(1)}} y_{ij} < 0$, and, together with condition (f-4) ($\lambda_{ij'}a_{ij'}n_{j'} < I_i$), we find the inequality

$$-\sum_{j\in B_i^{(1)}} y_{ij} \sum_{j'\in B_i^{(2)}} \lambda_{ij'}a_{ij'}n_{j'}y_{ij'} < -I_i \sum_{j\in B_i^{(1)}} y_{ij} \sum_{j'\in B_i^{(2)}} y_{ij'}. \tag{4.40}$$

Taking into account the term II-(1), we have

$$\text{II-(1)} + \text{II-(2)} = \Big(\sum_{l_i\in L_i^{(1)}} \sum_{l_i'\in L_i^{(1)}} + \sum_{l_i\in L_i^{(1)}} \sum_{l_i'\in L_i^{(2)}}\Big) J_{l_i l_i'} C_{l_i} y_{l_i} y_{l_i'} < \tag{4.41}$$

$$-n_i^2 I_i \sum_{j\in B_i^{(1)}} y_{ij}\Big(\sum_{j'\in B_i^{(1)}} + \sum_{j'\in B_i^{(2)}}\Big) y_{ij'} = 0. \tag{4.42}$$

We remark that the sum II-(1) + II-(2) tends to zero due to properties 1 and 2 of the perturbation equation. That is, this term eventually stops contributing to the quadratic form $dV/dt = W(\vec{y})$ for sufficiently large time.

II-(3): inactivated link - activated link Because the values of the Jacobi matrix in this double summation are zero, this summation vanishes.

II-(4): inactivated link - inactivated link The element of the Jacobi matrix $J_{(i,j),(i,j')}$ is zero for $j \neq j'$ and takes the value $\kappa(\lambda_{ij}a_{ij}n_j - I_i)$ for $j = j'$. Therefore

$$\sum_{l_i \in L_i^{(2)}} \sum_{l_i' \in L_i^{(2)}} J_{l_i l_i'} C_{l_i} y_{l_i} y_{l_i'} = \sum_{j \in B_i^{(2)}} \kappa(\lambda_{ij'} a_{ij'} n_{j'} - I_i) C_{ij} y_{ij}^2, \tag{4.43}$$

which is negative according to condition (f-4). We notice that this term also vanishes after eventually.

Taking all these results into account, we see that part II (foraging dynamics-foraging dynamics interactions) vanishes for $y_{mn} = 0$ $(\forall m, n)$ and is negative otherwise.

However, part II is negative due to the existence of perturbations to inactivated links. If we do not perturb inactivated foraging efforts or if all the effective links are activated at the fixed point (i.e., there are no inactivated links) or if we have waited long enough for all the perturbations to inactivated links to have vanished (this always happens regardless of how other variables behave), then part II (foraging dynamics-foraging dynamics interactions) makes no negative contribution to the quadratic form $dV/dt = W(\vec{y})$. This means in other words that activated links are not important for the negativeness of the quadratic form.

This is in contrast to part I (population dynamics-population dynamics interactions), where surviving species make a negative contribution to the quadratic form by $A_{ii} = 2J_{ii}C_i y_i^2 = -2\beta_i n_i C_i y_i^2$, that is independent of extinct species. If all the self competition strengths β_i are zero, we lose the negativeness result even if there are no extinct species or we do not perturb extinct species. For the foraging dynamics, the parameter κ plays a similar role to β in the population dynamics, because if $\kappa = 0$, we lose the contribution of the foraging dynamics. But for this reason, there is no difference between the cases $\kappa > 0$ and $\kappa = 0$ (for both cases the contribution to negativeness is zero).

Part III: foraging dynamics-population dynamics

We decompose the sum as

$$\sum_{m \in L} \sum_{n \in S} A_{mn} = \sum_{i \in S} \sum_{l_i \in L_i} \sum_{n \in S} A_{l_i n} \tag{4.44}$$

$$= \sum_{i \in S} \sum_{l_i \in L_i} A_{l_i i} + \sum_{i \in S} \sum_{l_i \in L_i} \sum_{\substack{n \in S \\ n \neq i}} A_{l_i n}. \tag{4.45}$$

Because the perturbations to extinct species $y_i, i \in \underline{S}$ and inactivated links $y_{ij}, j \in B_i^{(2)}$ eventually vanish, all we need to do is to treat the terms for surviving species

and activated links by assuming that we have waited for long enough that the influences of extinct species or inactivated links have disappeared. Therefore, we deal with

$$\underbrace{\sum_{i\in\overline{S}}\sum_{l_i\in L_i^{(1)}} A_{l_i i}}_{\text{III-(1)}} + \underbrace{\sum_{i\in\overline{S}}\sum_{l_i\in L_i^{(1)}}\sum_{\substack{n\in\overline{S}\\ n\neq i}} A_{l_i n}}_{\text{III-(2)}}, \tag{4.46}$$

with $y_i = 0$ for extinct species and $y_{ij} = 0$ for inactivated links. Part III-(1) represents the interactions between the population of a species N_i and its foraging efforts f_{ij} (a species and its links), and part III-(2) appears due to the interaction between the population of a species N_n and foraging efforts of other species f_{ij}(a species and links of other species).

III-(1): a species and its links Recalling the definition of $A_{l_i i}$,

$$A_{l_i i} = (J_{l_i i}C_{l_i} + J_{i l_i}C_i)y_{l_i}y_i, \tag{4.47}$$

and taking into account the values of the Jacobi matrix

$$J_{l_i i} = 0, \tag{4.48}$$

and

$$J_{i l_i} = \lambda_{ij}a_{ij}n_i n_j = I_i n_i, \tag{4.49}$$

we obtain

$$\sum_{i\in\overline{S}}\sum_{l_i\in L_i^{(1)}} A_{l_i i} = \sum_{i\in\overline{S}}\sum_{l_i\in L_i^{(1)}} (J_{l_i i}C_{l_i} + J_{i l_i}C_i)y_{l_i}y_i \tag{4.50}$$

$$= \sum_{i\in\overline{S}} I_i n_i C_i y_i \sum_{l_i\in L_i^{(1)}} y_{l_i} = 0. \tag{4.51}$$

This does not contribute to the negativeness of the quadratic form.

III-(2): a species and links of other species We decompose the summation as

$$\sum_{l_i\in L_i^{(1)}}\sum_{\substack{n\in\overline{S}\\ n\neq i}} = \sum_{l_i\in L_i^{(1)}}\sum_{\substack{n\in\overline{B}_i^{(1)}\\ n\neq i}} \tag{4.52}$$

$$= \underbrace{\sum_{(i,j)\in L_i^{(1)}}}_{\text{III-(2,a)}} + \underbrace{\sum_{(i,j)\in L_i^{(1)}}\sum_{\substack{n\in\overline{B}_i^{(1)}\\ n\neq i\\ n\neq j}}}_{\text{III-(2,b)}}, \tag{4.53}$$

where the first equality is obtained because the foraging dynamics of species i is affected only by the population size of its prey, and only the population dynamics of prey j includes the foraging effort of i.

III-(2,a) According to the element of the Jacobi matrix, we divide J_{l_ij} into two terms:

$$\begin{aligned} J_{l_ij} &= \kappa f_{ij}\lambda_{ij}a_{ij} - \kappa f_{ij}^2\lambda_{ij}a_{ij} && (4.54)\\ &:= J_{l_ij}^{(p)} + J_{l_ij}^{(q)}, && (4.55)\end{aligned}$$

$$J_{jl_i} = -a_{ij}n_in_j. \tag{4.56}$$

Then

$$\sum_{(i,j)\in L_i^{(1)}} A_{(i,j)j} = \sum_{j\in\overline{B}_i^{(1)}} (J_{(i,j)j}^{(p)}C_{ij} + J_{j(i,j)}C_j)y_{ij}y_j + \sum_{j\in\overline{B}_i^{(1)}} J_{l_ij}^{(q)}C_{ij}y_{ij}y_j, \tag{4.57}$$

where the second part will be treated later. Now we substitute the values of the Jacobi matrix into the first part:

$$\sum_{j\in\overline{B}_i^{(1)}} (J_{(i,j)j}^{(p)}C_{ij} + J_{j(i,j)}C_j)y_{ij}y_j = \sum_{j\in\overline{B}_i^{(1)}} (\kappa f_{ij}\lambda_{ij}a_{ij}C_{ij} - a_{ij}n_in_jC_j)y_{ij}y_j. \tag{4.58}$$

This will vanish if $\kappa f_{ij}\lambda_{ij}a_{ij}C_{ij} - a_{ij}n_in_jC_j = 0$, thus

$$C_{ij} = \frac{n_in_jC_j}{\kappa f_{ij}\lambda_{ij}}, \tag{4.59}$$

Or, recalling the equation $C_in_i\lambda_{ij} - C_jn_j = 0$,

$$C_{ij} = \frac{n_i^2C_i}{\kappa f_{ij}} > 0. \tag{4.60}$$

III-(2,b) The values of the Jacobi matrix are

$$\begin{aligned} J_{(i,j)n} &= -\kappa f_{in}\lambda_{in}a_{in}f_{ij} =: J_{(i,j)n}^{(q)} && (4.61)\\ J_{n(i,j)} &= 0. && (4.62)\end{aligned}$$

Now we estimate the summation together with the second term of (4.57):

$$\sum_{(i,j)\in L_i^{(1)}} \sum_{n\in\overline{B}_i^{(1)}} J_{(i,j)n}^{(q)}C_{ij}y_{ij}y_n = -\sum_{(i,j)\in L_i^{(1)}} \sum_{n\in\overline{B}_i^{(1)}} \kappa f_{in}\lambda_{in}a_{in}f_{ij}C_{ij}y_{ij}y_n. \tag{4.63}$$

Substituting the value of the coefficient C_{ij} (4.60), we obtain

$$\sum_{(i,j)\in L_i^{(1)}} \sum_{n\in\overline{B}_i^{(1)}} J_{(i,j)n}^{(q)}C_{ij}y_{ij}y_n = -\sum_{(i,j)\in L_i^{(1)}} y_{ij} \sum_{n\in\overline{B}_i^{(1)}} f_{in}\lambda_{in}a_{in}n_i^2C_iy_n, \tag{4.64}$$

which will eventually vanish because the sum of the perturbations to activated prey tends to zero due to property 1 of the perturbation equation. Again we remark

that this term is negative due to the perturbations to inactivated links as in part II.

We have now finished proving that the quadratic form $dV/dt = \sum_{m\in S\cup L}\sum_{n\in S\cup L} A_{mn}$ becomes negative for sufficiently large time and vanishes at the point where the perturbations are zero. Therefore, the fixed point is linearly stable.

What we have learned through the proof is that, as was mentioned above, the foraging dynamics does not make a negative contribution to the quadratic form. That is, the quadratic form is given by $dV/dt = \sum_{i\in S} A_{ii} = -2\sum_{i\in S}\beta_i n_i C_i y_i^2$. Therefore, if we set $\beta_i = 0$ for population dynamics, the quadratic term is not negative any more and we could lose the local stability of the fixed point. Therefore, it is important that $\beta_i > 0$ so that the quadratic form is negative, The only effect of the foraging dynamics is in equation 4.27: i.e., we obtain an equation $p_i\lambda_{ij} - p_j = 0$ only for activated links. By this effect, the topological condition was weakened from (p-3) to (f-5).

4.2 Global stability

In the previous section we investigated the conditions for local stability. Local stability of a fixed point means that all the trajectories near the fixed point approach the fixed point according to the dynamics. The set of all such trajectories is called basin of attraction of the fixed point. However, local stability does not give us any information about how large the basin of attraction is. Therefore, for example, it could happen that even if the positive fixed point (that is a fixed point where all the species are surviving) is locally stable, some species become extinct if we start from a point outside the basin of attraction. Thus a system with a locally stable positive fixed point does not have to be robust, i.e., we can not relate local stability to robustness.

Therefore, we investigate the possibility of global stability. By investigating global stability, we can say more about the robustness of a system: if a system has a globally stable positive fixed point, this system is perfectly robust, thus all the species can survive. In this section, we see that a fixed point (that satisfies the same conditions for species and foraging efforts as for local stability) is globally stable, i.e., all the trajectories in the phase space approach the fixed point, if the potential link structure of the original system L (not $\overline{L}$ or $\overline{L}^{(1)}$) satisfies Condition I. For the population dynamics with adaptive foraging, we need another condition: that the time scales of population dynamics and foraging dynamics are same, $\kappa = 1$.

The global stability of a fixed point is shown by finding a global Lyapunov function. We prove at first the uniqueness of the locally stable fixed point because the global stability of a fixed point and the existence of more than one locally stable fixed point contradict each other. The proof helps us to find the Lyapunov function.

4.2.1 Population dynamics without foraging dynamics

Uniqueness of locally stable fixed points

We denote a locally stable fixed point P by $(n_1^{(1)}, n_2^{(1)}, \cdots, n_s^{(1)})$, where $n_i^{(1)}$ is positive or zero. The local stability of the fixed point ensures that, if a species is extinct ($n_i^{(1)} = 0$), the growth rate of the species at the fixed point P is negative ($G_i^{(1)} < 0$), and the growth rates of the species with a positive population size ($n_i^{(1)} > 0$) are zero ($G_i^{(1)} = 0$) (see (p-1) and (p-2) in section 4.1). What will be shown in this subsection is that any fixed point Q $(n_1^{(2)}, n_2^{(2)}, \cdots, n_s^{(2)})$ other than P is unstable. This will be proved by showing that there is at least one species with a positive growth rate at the fixed point Q. This means that the fixed point Q is locally unstable, because it is necessary that all the growth rates at a fixed point must be zero or negative for a fixed point to be locally stable as mentioned in section 4.1.

Now we divide species S into four categories: $S = S_1 \cup S_2 \cup S_3 \cup S_4$. S_1 is the set of species that are extinct at both fixed points ($n_i^{(1)} = n_i^{(2)} = 0$), S_2 the set of species that are extinct at the first fixed point P but are surviving at the second fixed point Q ($n_i^{(1)} = 0$, $n_i^{(2)} > 0$), S_3 the set of species that are surviving at the first fixed point P but are extinct at the second fixed point Q ($n_i^{(1)} > 0$, $n_i^{(2)} = 0$) and S_4 the set of species that are surviving at both fixed points ($n_i^{(1)} > 0$, $n_i^{(2)} > 0$).

The anti-symmetrical structure of the population sizes and the growth rates ($n_i^{(1)} = 0 \Leftrightarrow G_i^{(1)} < 0$) and ($n_i^{(1)} > 0 \Leftrightarrow G_i^{(1)} = 0$) suggests the peculiar geometrical property of the fixed points. Indeed, if we plot a point $(n_i^{(1)}, G_i^{(1)})$ on the two dimensional $x - y$ plane, all the points are placed only on the positive part of the $x-$axis or the negative part of the $y-$axis. One method to investigate such a geometry is to consider an inner product in the phase space.

Therefore, we consider an inner product between the vector constructed from the differences of the population sizes $d\vec{n} = (n_1^{(2)} - n_1^{(1)}, n_2^{(2)} - n_2^{(1)}, \cdots, n_s^{(2)} - n_s^{(1)})$ and the vector constructed from the differences of the growth rates $d\vec{G} = (G_1^{(2)} - G_1^{(1)}, G_2^{(2)} - G_2^{(1)}, \cdots, G_s^{(2)} - G_s^{(1)})$. More precisely, we calculate the following (extended) inner product:

$$d\vec{n} \cdot d\vec{G} = \sum_{i \in S} C_i dn_i dG_i, \tag{4.65}$$

where $dn_i = n_i^{(2)} - n_i^{(1)}$ and $dG_i = G_i^{(2)} - G_i^{(1)}$.

We will show that there is a set of positive parameters C_i such that this inner product is negative. Because of the linearity of the growth rate, the difference of growth rates is equal to the "growth rate" of the difference of population sizes plus mortality α_i: $dG_i = G_i(d\vec{n}) + \alpha_i$. Substituting the values of the growth rates as a

function of population sizes, we find

$$\begin{aligned} d\vec{n}\cdot d\vec{G} &= d\vec{n}\cdot(\vec{G}(d\vec{n})+\vec{\alpha}) && (4.66)\\ &= \sum_{i\in B_i} C_i dn_i(G_i(d\vec{n})+\alpha_i) && (4.67)\\ &= \sum_{\substack{i\in S\\ j\in B_i}} \lambda_{ij}a_{ij}dn_j dn_i C_i - \sum_{\substack{i\in S\\ k\in R_i}} a_{ki}dn_k dn_i C_i - \sum_{i\in S}\beta_i dn_i^2 C_i && (4.68)\\ &= \sum_{i\in S}\sum_{j\in B_i}(\lambda_{ij}C_i - C_j)a_{ij}dn_j dn_i - \sum_{i\in S}\beta_i dn_i^2 C_i. && (4.69) \end{aligned}$$

Because of the topological condition, the equation $\lambda_{ij}C_i - C_j = 0$ has positive solutions. Therefore the inner product is negative:

$$d\vec{n}\cdot d\vec{G} = -\sum_{i\in S}\beta_i dn_i^2 C_i < 0. \tag{4.70}$$

On the other hand, according to the definition of the four categories S_1, S_2, S_3, S_4, some terms in the sum $d\vec{n}\cdot d\vec{G} = \sum_{i\in S} C_i dn_i dG_i$ vanish:

$$\begin{aligned} \sum_{i\in S_1} C_i(n_i^{(2)}-n_i^{(1)})(G_i^{(2)}-G_i^{(1)}) &= 0 && (4.71)\\ \sum_{i\in S_2} C_i(n_i^{(2)}-n_i^{(1)})(G_i^{(2)}-G_i^{(1)}) &= -\sum_{i\in S_2} C_i n_i^{(2)} G_i^{(1)} > 0 && (4.72)\\ \sum_{i\in S_3} C_i(n_i^{(2)}-n_i^{(1)})(G_i^{(2)}-G_i^{(1)}) &= -\sum_{i\in S_3} C_i n_i^{(1)} G_i^{(2)} && (4.73)\\ \sum_{i\in S_4} C_i(n_i^{(2)}-n_i^{(1)})(G_i^{(2)}-G_i^{(1)}) &= 0 && (4.74) \end{aligned}$$

Inequality (4.72) is obtained because of the negativeness of the growth rates $G_i^{(1)} < 0$ and the positiveness of the population size $n_i^{(2)} > 0$. In the equalities (4.72) and (4.73), we see the anti-symmetrical structure of the system. Therefore, the inner product can be reformulated as

$$d\vec{n}\cdot d\vec{G} = -\sum_{i\in S_2} C_i n_i^{(1)} G_i^{(2)} - \sum_{i\in S_3} C_i n_i^{(2)} G_i^{(1)}. \tag{4.75}$$

Together with inequality (4.70), we obtain

$$-\sum_{i\in S_3} C_i n_i^{(1)} G_i^{(2)} = \sum_{i\in S_2} C_i n_i^{(2)} G_i^{(1)} - \sum_{i\in S}\beta_i dn_i^2 C_i < 0, \tag{4.76}$$

that is to say

$$\sum_{i\in S_3} C_i n_i^{(1)} G_i^{(2)} > 0. \tag{4.77}$$

This shows us the fact that there exists at least one species in S_3 whose growth rate at the second fixed point Q is positive Because, if all the growth rates were negative,

the sum $\sum_{i\in S_3} C_i n_i^{(1)} G_i^{(2)}$ should be also negative because of the positiveness of the parameters C_i and population sizes $n_i^{(1)}$. Therefore the fixed point Q is unstable.

In the case where S_3 is the empty set, the sum $\sum_{i\in S_3} C_i n_i^{(1)} G_i^{(2)}$ vanishes and, looking at the inequality (4.76), $-\sum_{i\in S_2} C_i G_i^{(2)} n_i^{(1)}$ would be negative. But this contradicts inequality (4.72), which indicates that there does not exist such a fixed point.

Taking all these facts into account, we find that the fixed point P is the unique stable fixed point.

We notice that the point Q does not have to be a fixed point so that the inner product $d\vec{n}\cdot d\vec{G}$ is negative, which can be understood if we remember how the inequality (4.70) was obtained. To get the inequality (4.70) we use just the definition of the growth rate as a function of the population sizes and the topological condition that the equation $\lambda_{ij}C_i - C_j = 0$ has positive solutions.

Recalling the form of the population dynamics $dN_i/dt = N_i G_i$ and therefore that the (modified) superposition of the time derivative $\sum_i C_i dN_i/dt$ is obtained by the inner product of the vector of growth rates and population sizes $\vec{G}\cdot\vec{n}$, we are led to a Lyapunov function.

Existence of a Lyapunov function

We take an locally stable fixed point P and an arbitrary point Q $(N_1(t), N_2(t), \cdots, N_s(t))$ that is not a fixed point in the phase space. As was shown in the last subsection, the inner product of the two vectors $d\vec{n} = (N_1(t) - n_1^{(1)}, N_2(t) - n_2^{(1)}, \cdots, N_s(t) - n_s^{(1)})$ and $d\vec{G} = (G_1(t) - G_1^{(1)}, G_2(t) - G_2^{(1)}, \cdots, G_s(t) - G_s^{(1)})$ is zero if $d\vec{n} = \vec{0}$ i.e., $\vec{n}^{(1)} = \vec{N}$ and otherwise negative:

$$d\vec{n}\cdot d\vec{G} = \sum_{i\in S} C_i (N_i(t) - n_i^{(1)})(G_i(t) - G_i^{(1)}) < 0. \tag{4.78}$$

Substituting the equality $G_i(t) = \frac{1}{N_i}\frac{dN_i}{dt}$, we obtain the inequality

$$\sum_{i\in S} C_i (N_i(t) - n_i^{(1)})(\frac{1}{N_i}\frac{dN_i}{dt} - G_i^{(1)}) < 0. \tag{4.79}$$

The left-hand side can be further evaluated as

$$\sum_{i\in S} C_i (N_i - n_i^{(1)})(\frac{1}{N_i}\frac{dN_i}{dt} - G_i^{(1)}) = \sum_{i\in S} \frac{C_i(N_i - n_i^{(1)})}{N_i}\frac{dN_i}{dt} - \sum_{i\in \underline{S}} C_i N_i G_i^{(1)} < 0, \tag{4.80}$$

where $\underline{S}$ denotes the set of all the extinct species at the fixed point P. Because the growth rate of a species in $\underline{S}$ is negative, it follows that

$$\sum_{i\in S} \frac{C_i(N_i - n_i^{(1)})}{N_i}\frac{dN_i}{dt} < 0. \tag{4.81}$$

The left-hand side of (4.81) is the time derivative of the scalar function

$$V(\vec{N}) = \sum_{i\in S} C_i \int \frac{(N_i - n_i^{(1)})}{N_i} dN_i, \tag{4.82}$$

$$= \sum_{i\in S} C_i (N_i - n_i^{(1)} \log N_i) \tag{4.83}$$

which takes its minimum value at $N_i = n_i$. So it turns out that, if the potential link structure satisfies the topological condition $\lambda_{ij}C_i - C_j = 0$, a locally stable fixed point is globally stable. We notice that, if the potential link structure satisfies the topological condition, the positive fixed point (i.e., a fixed point where all the species are surviving) is automatically locally stable because all the conditions (p-1)-(p-3) are satisfied and is, therefore, globally stable if it exists. Thus, in this case, the question is only whether the system has a positive fixed point or not.

4.2.2 Population dynamics with foraging dynamics

Uniqueness of locally stable fixed points

In the system of population dynamics with foraging dynamics, not only the species but all the links have dynamics and we have to consider the stability of all the variables at once. In order to do this, we introduce a new variable that is the sum of the growth rates of population dynamics and a links:

$$H_{ij} = G_i + F_{ij}, \tag{4.84}$$

where F_{ij} is the growth rate of the foraging dynamics of link (i, j). If the fixed point is locally stable, the variable H_{ij} takes a negative value for all links and, if there exists a link where H_{ij} is positive, the fixed point is unstable. If we express the variable H_{ij} as a function of population sizes, we have

$$H_{ij} = G_i + F_{ij} \tag{4.85}$$

$$= \lambda_{ij} a_{ij} N_j - \sum_{k\in R_i} a_{ki} f_{ki} N_k - \alpha_i - \beta_i N_i. \tag{4.86}$$

For convenience, we denote the product $f_{ij}N_i$ by z_{ij} and we write the vector forms of H_{ij} and z_{ij} as $\vec{H}$ and $\vec{z}$. We notice that the dimension of the vectors is the number of links L.

Now we consider two fixed points P $(n_1^{(1)}, \vec{f}_1^{(1)} n_2^{(1)}, \vec{f}_2^{(1)}, \cdots, n_s^{(1)}, \vec{f}_s^{(1)})$ and Q $(n_1^{(2)}, \vec{f}_1^{(2)}, n_2^{(2)}, \vec{f}_2^{(2)}, \cdots, n_s^{(2)}, \vec{f}_s^{(2)})$ and assume that the fixed point P is locally stable.

Cleary, this system has a similar geometrical structure to the system with population dynamics only (previous subsection), because $z_{ij} > 0 \Leftrightarrow H_{ij} = 0$ and $z_{ij} = 0 \Leftrightarrow H_{ij} < 0$, thus all the points (z_{ij}, H_{ij}) must be placed on the positive part of the $x-$axis or the negative part of the $y-$axis in the $x - y$ plane. We define an inner product of the two vectors $d\vec{H} = \vec{H}^{(2)} - \vec{H}^{(1)}$ and $d\vec{z} = \vec{z}^{(2)} - \vec{z}^{(1)}$ by

$$d\vec{z} \cdot d\vec{H} = \sum_{i\in S} \sum_{j\in B_i} C_{ij} dz_{ij} dH_{ij}. \tag{4.87}$$

Now we show that there is a set of parameters C_{ij} that makes this inner product negative. If we see the variables H_{ij} as functions of population sizes n_i and foraging efforts f_{ij}, the inner product can be written as

$$\begin{aligned} d\vec{z} \cdot d\vec{H} &= \sum_{\substack{i\in S \\ j\in B_i}} \lambda_{ij} a_{ij} dn_j dz_{ij} C_{ij} && (4.88) \\ &- \sum_{\substack{i\in S \\ j\in B_i \\ k\in R_i}} a_{ki} dz_{ki} dz_{ij} C_{ij} && (4.89) \\ &- \sum_{\substack{i\in S \\ j\in B_i}} \beta_i dn_i dz_{ij} C_{ij}. && (4.90) \end{aligned}$$

If we change the order of the sum in the second term, we get

$$\begin{aligned} \text{The second term} &= \sum_{k\in S} \sum_{i\in B_k} a_{ki} dz_{ki} \sum_{j\in B_i} dz_{ij} C_{ij} && (4.91) \\ &= \sum_{i\in S} \sum_{j\in B_i} a_{ij} dz_{ij} \sum_{m\in B_j} dz_{jm} C_{jm}. && (4.92) \end{aligned}$$

For the second equality, we just replaced the index (k, i, j) by (i, j, m). Then the first term and the second term in the inner product can be combined as

$$(4.88) + (4.89) = \sum_{\substack{i\in S \\ j\in B_i}} a_{ij} dz_{ij} (\lambda_{ij} dn_j C_{ij} - \sum_{m\in B_j} dz_{jm} C_{jm}). \quad (4.93)$$

By substituting the relation $dn_j = \sum_{m\in B_j} dz_{jm}$ into dn_j, this term can be simplified to

$$(4.88) + (4.89) = \sum_{\substack{i\in S \\ j\in B_i}} a_{ij} dz_{ij} \sum_{m\in B_j} (\lambda_{ij} C_{ij} - C_{jm}) dz_{jm}. \quad (4.94)$$

This term will vanish because the topological condition ensures that the equation system $\lambda_{ij} C_{ij} - C_{jm} = 0$ for i and j has positive solutions.

This structure of the equation system imposes a further constraint for the parameters C_{im}. Because the term $\lambda_{ij} C_{ij}$ does not depend on m, C_{jm} has to be independent of prey m of species j and this constraint must be imposed on all the species. Thus each species has only one parameter: $C_{ij} =: C_i$.

Then the sum over j in the third term (4.90) can be removed because the coefficients $\beta_i C_i$ do not include index j:

$$\begin{aligned} d\vec{z} \cdot d\vec{H} &= -\sum_{i\in S} \sum_{j\in B_i} \beta_i dn_i dz_{ij} C_i && (4.95) \\ &= -\sum_{i\in S} \beta_i C_i dn_i \sum_{j\in B_i} dz_{ij} && (4.96) \\ &= -\sum_{i\in S} \beta_i C_i dn_i^2 < 0 && (4.97) \end{aligned}$$

where we again used the relation $dn_i = \sum_{j \in B_i} dz_{ij}$ for the third equality.

In a similar way to what was done in the investigation of population dynamics without foraging dynamics, we divide all the links into four categories :$L = L_1 \cup L_2 \cup L_3 \cup L_4$ and find that some terms in the sum $d\vec{z} \cdot d\vec{H} = \sum_{i \in S} \sum_{j \in B_i} C_i dz_{ij} dH_{ij}$ can be dropped:

$$\sum_{(i,j) \in L_1} C_i (z_{ij}^{(2)} - z_{ij}^{(1)})(H_{ij}^{(2)} - H_{ij}^{(1)}) = 0 \tag{4.98}$$

$$\sum_{(i,j) \in L_2} C_i (z_{ij}^{(2)} - z_{ij}^{(1)})(H_{ij}^{(2)} - H_{ij}^{(1)}) = -\sum_{(i,j) \in L_2} C_i z_{ij}^{(2)} H_{ij}^{(1)} > 0 \tag{4.99}$$

$$\sum_{(i,j) \in L_3} C_i (z_{ij}^{(2)} - z_{ij}^{(1)})(H_{ij}^{(2)} - H_{ij}^{(1)}) = -\sum_{(i,j) \in L_3} C_i z_{ij}^{(1)} H_{ij}^{(2)} \tag{4.100}$$

$$\sum_{(i,j) \in L_4} C_i (z_{ij}^{(2)} - z_{ij}^{(1)})(H_{ij}^{(2)} - H_{ij}^{(1)}) = 0 \tag{4.101}$$

$$\tag{4.102}$$

As a result, we obtain

$$-\sum_{(i,j) \in L_3} C_i z_{ij}^{(1)} H_{ij}^{(2)} = \sum_{(i,j) \in L_2} C_i z_{ij}^{(2)} H_{ij}^{(1)} - \sum_{i \in S} \beta_i C_i (n_i^{(2)} - n_i^{(1)})^2 < 0, \tag{4.103}$$

or

$$\sum_{(i,j) \in L_3} C_i z_{ij}^{(1)} H_{ij}^{(2)} > 0 \tag{4.104}$$

Therefore, there exists a link (i, j) where the variable $H_{ij}^{(2)}$ is positive. Because of the definition of the variable $H_{ij} = G_i + F_{ij}$, this means that at the fixed point Q, the growth rate $G_i^{(2)}$ of species i is positive or the growth rate of the foraging effort $F_{ij}^{(2)}$ is positive. Therefore the fixed point Q is unstable. We notice that this result is so strong that, if P is a positive fixed point and Q is a positive fixed point with a different effective link structure, Q is unstable. That is to say, there can exist only one locally stable fixed point among 2^{S+L} fixed points. The uniqueness is valid for any κ, since the value of κ does not play any role in the calculations.

Existence of a Lyapunov function

We can find a Lyapunov function for the coupled system of the population dynamics and the foraging dynamics for the case of $\kappa = 1$, because the time derivative of the variable $z_{ij} = f_{ij} N_i$ will be given by the product of the variable z_{ij} and the function H_{ij}:

$$\frac{dz_{ij}}{dt} = f_{ij} \frac{dN_i}{dt} + N_i \frac{f_{ij}}{dt} \tag{4.105}$$

$$= f_{ij} N_i G_i + f_{ij} N_i F_{ij} \tag{4.106}$$

$$= f_{ij} N_{ij} (G_i + F_{ij}) \tag{4.107}$$

$$= z_{ij} H_{ij}. \tag{4.108}$$

If we regard the function H_{ij} as the growth rate of the variable z_{ij}, it turns out that this system has the same structure as the system with population dynamics only.

The description of the system with variables N_i and f_{ij} and the description of the system with variable z_{ij} are equivalent if we set the initial values of foraging efforts so that they sum up to one over the prey of a species ($\sum_{j\in B_i} f_{ij}(0) = 1$), and if all the species have positive population sizes. The second condition will be satisfied if we choose as the initial condition of the system a point where all the species have positive population sizes, because, in that case, the system never reaches a point where there exists a species whose population size is exactly zero (the trajectory can only come close to such a point). In fact, if the above conditions are satisfied, the values of N_{ij} and f_{ij} are uniquely obtained from the value of z_{ij} by the transformation

$$N_i(t) = \sum_{j\in B_i} z_{ij}(t) \tag{4.109}$$

$$f_{ij}(t) = \frac{z_{ij}(t)}{\sum_{j\in B_i} z_{ij}(t)}. \tag{4.110}$$

Now we take the point Q as an arbitrary point $(n_1(t), \vec{f}_1(t), n_2(t), \vec{f}_2(t), \cdots, n_s(t), \vec{f}_s(t))$ in the phase space. Then the inner product of the two vectors $d\vec{z}$ and $d\vec{H}$ is zero if $\vec{z} = \vec{z}^{(1)}$ and otherwise negative:

$$d\vec{z}\cdot d\vec{H} = \sum_{i\in S}\sum_{j\in B_i} C_i(z_{ij}(t) - z_{ij}^{(1)})(H_{ij}(t) - H_{ij}^{(1)}) < 0. \tag{4.111}$$

Substituting the equality $H_{ij}(t) = \frac{1}{z_{ij}}\frac{dz_{ij}}{dt}$ into the definition of the inner product, we obtain

$$d\vec{z}\cdot d\vec{H} = \sum_{i\in S}\sum_{j\in B_i} C_i(z_{ij} - z_{ij}^{(1)})(\frac{1}{z_{ij}}\frac{dz_{ij}}{dt} - H_{ij}^{(1)}), \tag{4.112}$$

which can be further evaluated as

$$d\vec{z}\cdot d\vec{H} = \sum_{i\in S}\sum_{j\in B_i} \frac{C_i(z_{ij} - z_{ij}^{(1)})}{z_{ij}}\frac{dz_{ij}}{dt} - \sum_{i\in S}\sum_{j\in B_i} C_i H_{ij}(z_{ij} - z_{ij}^{(1)}). \tag{4.113}$$

The sum of the second part of the right-hand side is negative because $H_{ij} = 0$ if and only if $z_{ij}^{(1)} > 0$ (i.e., $f_{ij}^{(1)} > 0$ and $n_i^{(1)} > 0$), and $H_{ij} < 0$ if $z_{ij} = 0$ (i.e., $f_{ij}^{(1)} = 0$ or $n_i^{(1)} = 0$) and because $z_{ij} > 0$. Together with the fact that the inner product is negative, we see that the first part of the right-hand side is negative:

$$\sum_{i\in S}\sum_{j\in B_i} \frac{C_i(z_{ij} - z_{ij}^{(1)})}{z_{ij}}\frac{dz_{ij}}{dt} < 0, \tag{4.114}$$

and the left-hand side is the time derivative of the scalar function

$$V(\vec{z}) = \sum_{i\in S}\sum_{j\in B_i} C_i \int \frac{(z_{ij} - z_{ij}^{(1)})}{z_{ij}} dz_{ij}, \tag{4.115}$$

$$= \sum_{i\in S}\sum_{j\in B_i} C_i (z_{ij} - z_{ij}^{(1)} \log z_{ij}). \tag{4.116}$$

So we saw in this section that if the topology of a food web satisfies Condition I (4.19), (i) there exists only one locally stable fixed point (ii) the fixed point is also globally stable, i.e., regardless of the initial condition, all trajectories approach the fixed point. In this case, the system never shows chaotic or even periodic behavior, but only stationary behavior. Therefore the system has a perfect constancy. In the next section, we investigate the stability of fixed points and the dynamics of a small system that does not satisfy Condition I.

4.3 Small system

In section 4.1 we proved that there is a set of parameters C_i such that the time derivative $W(\vec{y}) = dV(\vec{y})/dt$ of the positive Lyapunov function $V(\vec{y}) = \sum_m C_m {y_m}^2$ for a system satisfying conditions (p-1)-(p-3) (for only population dynamics) and (f-1)-(f-5) (for a coupled system of population dynamics with foraging dynamics) is negative-definite. The proof was done by showing that all the terms that could make the quadratic form $W(\vec{y})$ positive eventually vanish. In the proof, we saw that only the square terms of population dynamics (i.e., $\sum_{i\in S} 2J_{ii}C_i {y_i}^2$ with $J_{ii} = -\beta_i n_i$) make a negative contribution to the quadratic form $dV/dt = W(\vec{y})$, which makes the fixed point locally stable even in the case where foraging dynamics is introduced. Since such negative terms include the parameter β_i, we expect that these parameters play an important role in the local stability of fixed points, even if the system does not satisfy Condition I.

There is a similar argument for the global stability. The point is that we can find a set of parameter C_i which makes the inner product $d\vec{n} \cdot d\vec{G}$ (for population dynamics only) or $d\vec{z} \cdot d\vec{H}$ (for population dynamics and foraging dynamics) negative. For both cases the self competition terms of the population dynamics played an important role ((4.70) and (4.97)).

In this section, we numerically investigate the stability of the positive fixed point of a small system (described by population dynamics with or without foraging dynamics) whose potential link structure does not satisfy Condition I in order to learn about the effect of the intraspecific competition strength β.

Positive fixed point and local stability

The potential link structure of the example is illustrated in Figure 4.2 (a). This system has four species $(N_1, \cdots, N_4)$ and one external resource with a fixed population size (E). In this system, only the third species N_3 has more than one potential prey, and thus only the species N_3 performs foraging dynamics if we include foraging dynamics in the model.

Only the link structure (a) corresponds to a positive fixed point of population dynamics without foraging, thus the configuration $(\overline{S} = S, L_a)$ must be stable so that the positive fixed point (or the full surviving pattern $\overline{S} = S$) is stable. To a positive fixed point of the coupled system of population dynamics with foraging dynamics, there correspond three effective link structures denoted by L_a (Figure 4.2 (a)), L_b (Figure 4.2 (b)) and L_c (Figure 4.2 (c)). For link structure L_a, both foraging efforts f_{31} and f_{32} have to be positive and smaller than unity at the fixed point. For link structures L_b and L_c, one foraging effort is exactly 1 and the other is zero at the fixed point. If one of the configurations $(\overline{S} = S, L_a)$, $(\overline{S} = S, L_b)$ or $(\overline{S} = S, L_c)$ is stable, the full surviving pattern $\overline{S} = S$ is stable.

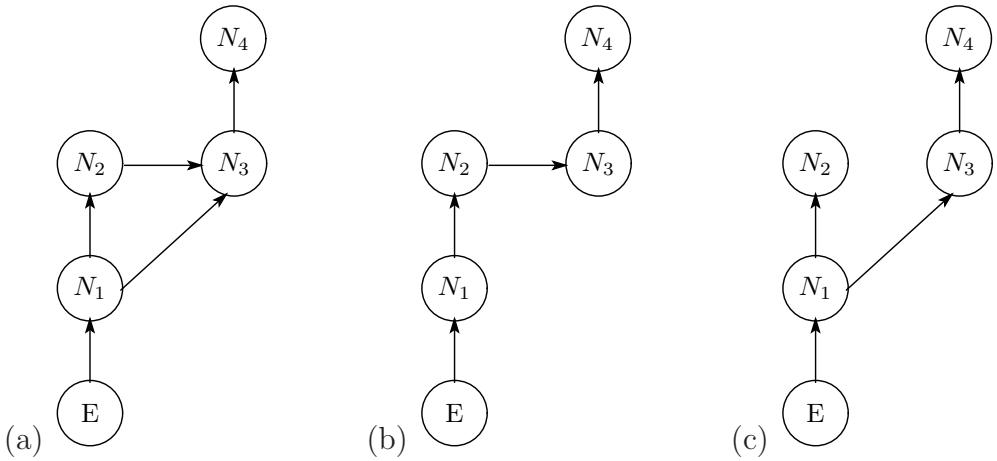


Figure 4.2: (a): Potential link structure L_a. If the system has a positive fixed point with finite foraging effort $0 < f_{31} < 1$, this is also an effective link structure. (b): Effective link structure L_b with $f_{31} = 0$. (c): Effective link structure L_c with $f_{31} = 1$. E denotes the external resource with a fixed population size.

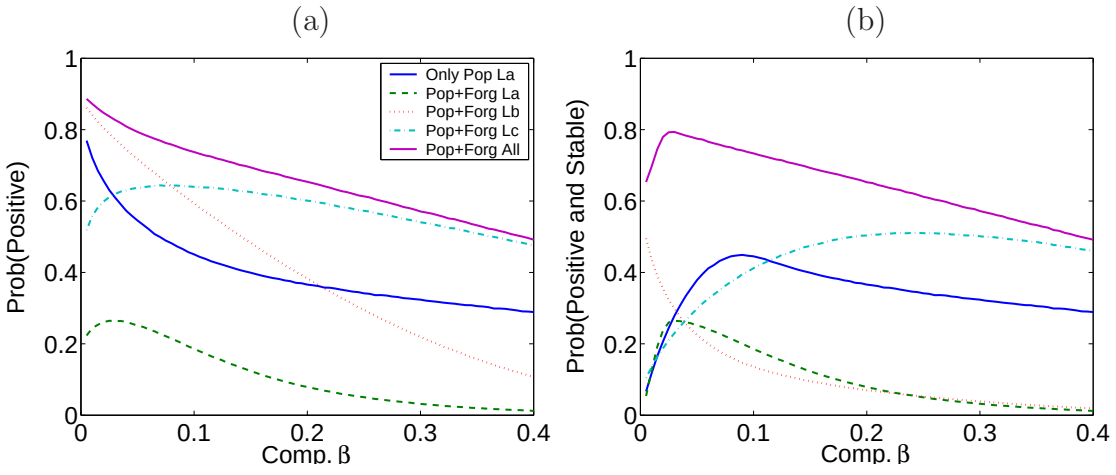


Figure 4.3: (a): The probability that a system has a positive fixed point $(N_1 > 0, N_2 > 0, N_3 > 0, N_4 > 0)$. (b): The probability that a system has a stable fixed point.

Not all webs have a positive fixed point $(N_1 > 0, N_2 > 0, N_3 > 0, N_4 > 0)$ (i.e., a fixed point where all the species are alive). Whether a system has a positive

fixed point depends on the parameters of the system (connection strength, etc.). In Figure 4.3 (a), we plot the probabilities that the classical population dynamics with link structure L_a or population dynamics with adaptive foraging and effective link structure L_a, L_b or L_c have a positive fixed point as a function of the competition strength β. Here β is assumed to be the same for all species.

This plot was obtained by generating $5 \cdot 10^5$ webs with various connection strength and sizes of the external resource E and solving the equation systems $G_1 = 0, G_2 = 0, G_3 = 0, G_4 = 0$ (for the classical population dynamics), $G_1 = 0, G_2 = 0, G_3 = 0, G_4 = 0, F_{31} = 0, f_{31} + f_{32} = 1$ (for the population dynamics with adaptive foraging with the link structure L_a), $G_1 = 0, G_2 = 0, G_3 = 0, G_4 = 0, f_{31} = 0, f_{32} = 1$ (for the population dynamics with adaptive foraging with the link structure L_b) or $G_1 = 0, G_2 = 0, G_3 = 0, G_4 = 0, f_{31} = 1, f_{32} = 0$ (for the population dynamics with adaptive foraging with the link structure L_c).

We then counted the number of webs where there is a positive solution (legend " Only Pop La", "Pop + Forg Lb" and "Pop + Forg Lc") or where there is a positive solution with a positive foraging effort smaller than unity ($0 < f_{31} < 1$) (Legend "Pop+Forg La"). The values of the connection strength were randomly chosen from the range $(0, 1]$ and the size of the external resource E from the range $(0, 2]$ for each sample of webs. The mortality α in the equation system was fixed at 0.02. The legend "Pop+Forg All" in the figure indicates the probability that the coupled system of population dynamics with foraging dynamics has a positive fixed point in one of the three effective link structures L_a, L_b and L_c, i.e., the probability that the full surviving pattern can be achieved.

We see that both probabilities of population dynamics with or without foraging dynamics with legend " Only Pop La" or "Pop+Forg All" monotonically decrease. This is understandable if we consider the meaning of the parameter β, that is, a intraspecific competition. As the intraspecific competition becomes larger, it is more difficult for the system to have a positive fixed point. We notice that the probability of "Pop+Forg All" is smaller than the sum of the probabilities of "Pop+Forg La", "Pop+Forg Lb" and "Pop+Forg Lc". This shows us the fact that there can exist more than two positive fixed points in the system of population dynamics and foraging dynamics.

Figure 4.3 (b) shows the probabilities that the system has a locally stable positive fixed point for each configuration. This plot was obtained by calculating the eigenvalues of the Jacobi matrix at the fixed points, and we counted the number of examples where all real parts of the eigenvalues are negative. These probabilities are of course in general smaller than the probabilities of Figure 4.3 (b).

We see that the probability that a web with adaptive foraging has a stable positive fixed point is always larger than for a web without adaptive foraging. Thus, statistically, a system with adaptive foraging is more stable than without foraging. This does not mean, however, that a food web for which the population dynamics without foraging has a stable positive fixed point always implies that the web is stable if the foraging dynamics is incorporated. In fact we can find a set of parameter values for which the population dynamics without foraging dynamics has stable positive fixed point while the population dynamics with foraging dynamics does not.

One considerable point is that the probabilities of " Only Pop La" and "Pop+Forg All" in Figure 4.3 (b) get closer to the probabilities with the same legends in Figure 4.3 (a) as β becomes larger. This means that, for large values of β, "the system has a positive fixed point" means "the positive fixed point is locally stable", which shows us that the parameter β actually stabilizes already existing fixed points, which can be expected from the argument of the first part of this section. In fact if we plot the ratio of the probabilities $Prob$(Positive)/$Prob$(Positive and Stable) from the figures 4.3 (a) and (b), this ratio monotonically increases as a function of β (not shown).

Another point is that, for the case of population dynamics with adaptive foraging, the probability of "Pop+Forg All" is exactly same as the sum of the three probabilities of "Pop+Forg La", "Pop+Forg Lb" and "Pop+Forg Lc". Thus the system has only one locally stable fixed point, i.e., only one of the configurations $(\overline{S} = S, L_a)$, $(\overline{S} = S, L_b)$ and $(\overline{S} = S, L_c)$ can be stable, which is the same result shown in the previous section 4.2. But here the potential link structure L_a does not satisfy Condition I (4.19), even though this link structure is close to a link structure that satisfies the condition, in the sense that it is only the presence of one extra link, $(3, 1)$ or $(3, 2)$, that breaks the condition. Actually Condition I is a sufficient condition for the uniqueness of fixed points. Therefore, we might expect the existence of a weaker condition which depends on the parameter values (e.g., β) of the system.

We also notice that the probability of " Only Pop Lc" is much larger than the other two. The topological differences of this link structure to other two are (i) the topology is simpler than that of L_a, (ii) the shortest chain length of L_c (3) is smaller than that of L_b (4). This result indicates to us that a stable configuration is more likely to have a simple structure.

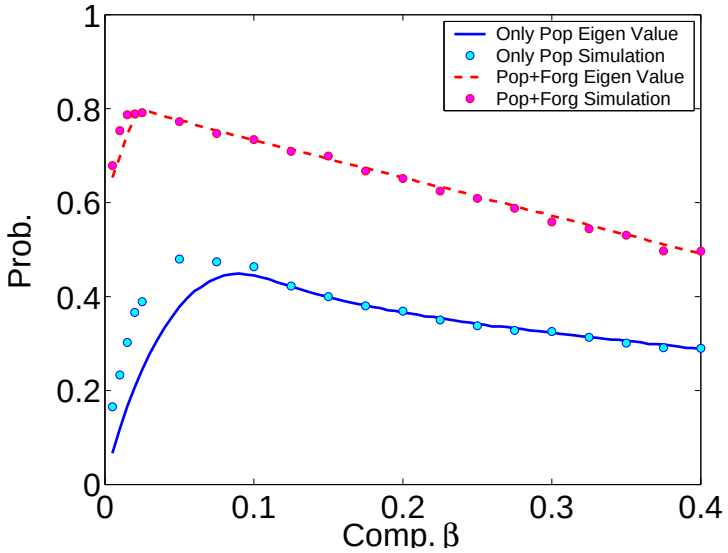


Figure 4.4: The probabilities that the system has a stable fixed point (lines, same as Figure 4.3 (b)) and the probabilities that a trajectory of the differential equation approaches the positive fixed point (dots) for only pop. and pop.+forg..

Numerical simulation

In Figure 4.4 we plot the probabilities that a trajectory with a randomly chosen initial condition approaches a positive fixed point according to the differential equations (4.1) or (4.3) (i.e., the probabilities that all the species survive in the end, or in other words, the probabilities that the systems are perfectly robust) by blue dots (only population dynamics) and red dots (population dynamics with adaptive foraging). This plot was obtained by numerically simulating the dynamical equations.

To compare these results with the probabilities that the system has a stable fixed point, we also plotted the probabilities found in Figure 4.3 (b) with " Only Pop La" and "Pop+Forg All" by a blue line and a red line. What we find in the figure is that, for larger values of β, the result of numerical integration and the local stability analysis agree with each other (lines and dots).

If a fixed point is only locally stable, which can be determined from the eigenvalues of a fixed point, the probability with the legend "Eigen Value" must be larger than the probability with legend"Simulation", because, even if the fixed point is stable, the trajectory may not approach the fixed point and the inverse of this statement is not valid (it is not possible that a trajectory approaches an unstable fixed point). Therefore, the plot shows us the global stability of fixed points for larger β.

The mismatches for small values of β appear because it is possible that all the species survive, even if the positive fixed point is unstable. This is possible when the system behaves periodically or chaotically. We expect, therefore, that the systems show bifurcations for small values of β. In fact, we find the bifurcation diagrams shown in Figure 4.5 (bifurcation of the classical population dynamics) and 4.6 (bifurcation of the population dynamics with adaptive foraging).

To make the bifurcation diagram 4.5 we fixed the parameter values of the system to $(a_{21}, a_{32}, a_{32}, a_{43}) = (0.9, 0.77, 0.52, 0.6)$ and $E = 0.5$. These parameter values were determined such that the system has always a positive fixed point for all values of β in the range $[0.02, 0.1]$. To obtain the plot, we numerically integrated the population dynamics and detected the local maxima and minima of the time series of population size $N_1(t)$ for $t > 50000$ for each value of β. Then we plotted the values of these local minima and maxima for each value of β as a point in the figure.

As we expected, bifurcation occurs for small values of β. One remarkable point is that the time series of $N_1(t)$ can take very small values for small values of β, and the minimal value becomes smaller and smaller as the value of β decreases. If we set an extinction threshold in the simulation, the species is more likely to become extinct as β decreases. We did not find chaotic behavior but only periodic behavior in this parameter range.

Figure 4.6 is a bifurcation diagram with parameters $E = 0.5$ and $(a_{21}, a_{32}, a_{32}, a_{43})$ $= (0.9, 0.77, 0.52, 0.6)$. The first bifurcation (Hopf-bifurcation) occurs at a smaller value of $\beta \simeq 0.013$ (point A) than for population dynamics without adaptive foraging, even though it could be difficult to recognize that a bifurcation occurs at the point A from the figure. That is, in order for the population dynamics with

adaptive foraging to show non-stationary behavior, we have to set the value of β smaller than for population dynamics without foraging dynamics. However, once the first bifurcation has occurred, the behavior of the system becomes much more complicated than for population dynamics only. It seems in the figure that there is a discontinuous jump at the point B, but the bifurcation actually occurs continuously, which is difficult to see in the figure. In the range between the points B and C, we see a period-doubling bifurcation. We found that the ratio of each bifurcation interval in this range is 5.9, which is not the same as the Feigenbaum constant. Considering the time series of the effort $f_{31}(t)$ for a small value of β, where chaotic behavior is observed, we find that the effort $f_{31}(t)$ switches from zero to one very quickly from time to time, i.e., the system switches from L_b to L_c and vice versa. The time intervals in which L_a is observed are very small.

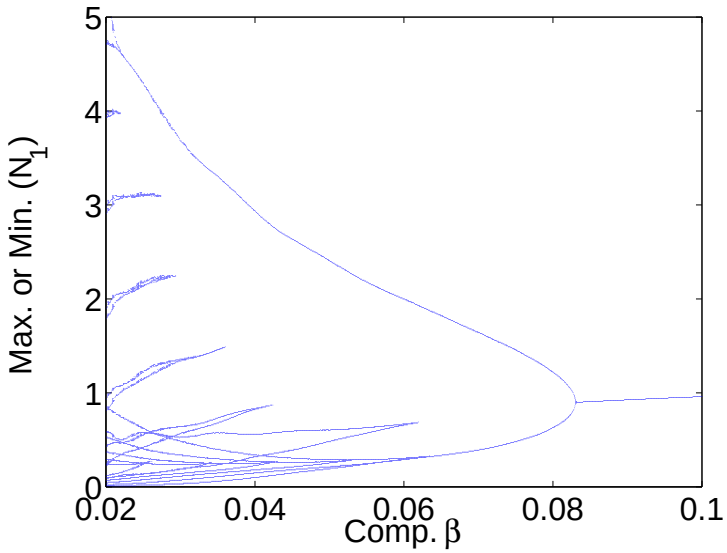


Figure 4.5: Bifurcation of population dynamics without foraging dynamics. This figure was obtained by detecting local maxima and minima of the time series of the population size $N_1(t)$. The parameter values are fixed at $(a_{21}, a_{32}, a_{32}, a_{43}) = (0.9, 0.77, 0.52, 0.6)$ and $E = 0.5$.

4.4 Conclusion

In this chapter we found a topological condition under which food webs are stable, i.e., the population dynamics of Lotka-Volterra type with or without adaptive foraging has a (locally or globally) stable fixed point. The condition includes what the Quirk-Ruppert theorem offers and, in addition, we have shown that the absence of an omnivore or perfect ecological efficiency ($\lambda_{ij} = 1$) makes the system stable (Condition I, Figure 4.1). In terms of local stability, Condition I applies to the effective link structure for population dynamics with adaptive foraging. Food webs are more likely to achieve an effective link structure which satisfies the condition, and are therefore stable, as the average number of prey per species K increases.

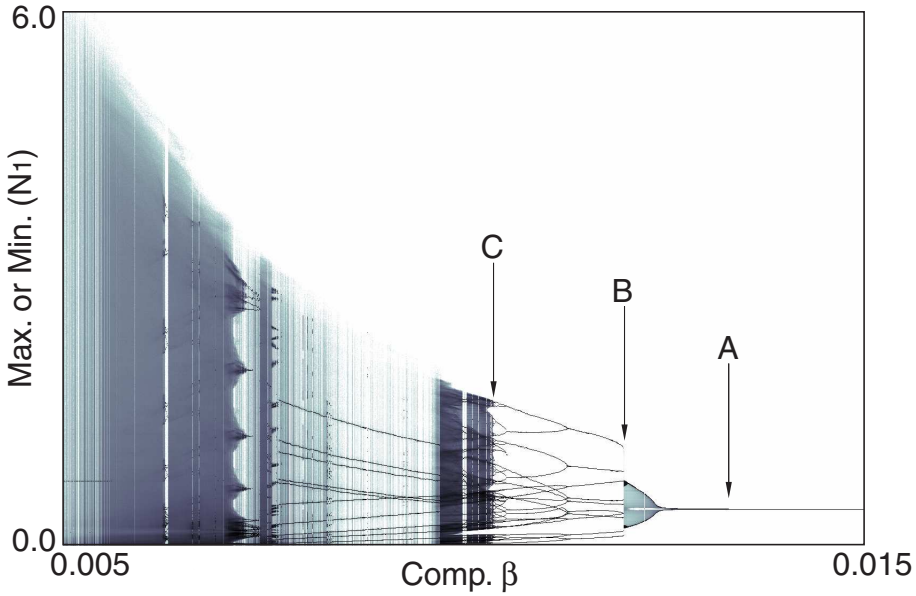


Figure 4.6: Bifurcation of population dynamics with foraging dynamics. This figure was obtained by detecting local maxima and minima of the time series of the population size $N_1(t)$. $(a_{21}, a_{32}, a_{32}, a_{43}) = (0.62, 0.39, 0.87, 0.93)$ and $E = 0.16$.

We also found that a fixed point of the population dynamics whose potential link structure satisfies Condition I is not only locally stable but also globally stable. This result is still true if the population dynamics is combined with adaptive foraging, if the time scales of population dynamics and foraging dynamics are the same. We were able to show the uniqueness of fixed points for arbitrary values of κ. In the literature, a matrix A, for which there exists a positive diagonal matrix C such that $CA + A^TC$ is negative definite, is called Volterra-Lyapunov stable. In section 4.1.1, we have shown that the Jacobi matrix J is Volterra-Lyapunov stable if the link structure satisfies Condition I. It is already known that a fixed point of a classical Lotka-Volterra system with a Volterra-Lyapunov stable community matrix A defined by $A_{ij} = \lambda_{ij}a_{ij}, A_{ik} = -a_{ki}, A_{ii} = -\beta_i$ is globally stable (Takeuchi, 1996). As we have shown, a community matrix of a food web that satisfies Condition I is always Volterra-Lyapunov stable, but the converse is not valid. Therefore, the next step would be to investigate whether a food web with a Volterra-Lyapunov stable community matrix has a globally stable fixed point if adaptive foraging is implemented.

Finally, we also showed the importance of intraspecific competition for stability by investigating a small system. Even when the link structure does not satisfy Condition I, a fixed point can be globally stable for larger values of β.

Factors that have not yet been investigated and would be interesting are the effects of interspecific competition, handling time and the nonlinearity of constraints on foraging efforts. It has been reported that interspecific competition as well as handling time can lead to the instability of fixed points of classical population dynamics and can induce complex dynamical behavior such as chaos (Williams and Martinez, 2004; Vano et al., 2006). However, there is no result yet about the

combination of population dynamics, adaptive foraging, interspecific competition or handling time. The effects of nonlinear constraints on foraging efforts could be different to the effects of linear constraints, because the potential and effective link structures are the same in the case of nonlinear constraints. However, there are not yet any results concerning the effects of nonlinear constraints.

Chapter 5

Stability under Evolution

A food web obtains a new species from time to time due to the immigration of a new species or speciation in an already existing species. Such introductions of new species occur on longer time scales than population dynamics or adaptive dynamics. In terms of speciation, one or a few individuals of a species will change their feature or niche in food webs, therefore the composition and the linkage patterns of food webs also change. Such long-term changes of the composition and the linkage patterns affect food webs in two different ways. First, a complex food web will be produced by a series of introductions of new species. In this case, an evolutionary model can be seen as an algorithm for obtaining a complex food web. The second point is that the introduction of a new species is a perturbation to the already existing food web. After population dynamics, several species may become extinct due to the introduction of the new species. Consequently long-term changes of topological web patterns may break food webs.

Our purpose in this chapter is to study the stability of model food webs with and without foraging dynamics under such topological changes. Therefore, we assume that initially there is an existing food web with several trophic levels and assume a layer structure as an initial topology, i.e., species in level l feed only on species in level $l-1$ (Figure 4.1 (c)). We change connection patterns of webs with a much longer time scale than that of population dynamics as is done in the literature (Caldarelli et al., 1998; Drossel et al., 2001; Bastolla et al., 2001; Bastolla et al., 2002; Drossel et al., 2004). Our interest is in investigating whether a food web with several trophic levels (> 2) can be sustained. If this is possible, the model food web is said to be stable under evolution. We base our work on the evolutionary model proposed by Lässig et al. (2001) and Bastolla et al. (2002). As was mentioned in chapter 1, these authors did not include adaptive foraging in their model and showed the results of computer simulations only with one trophic level (i.e., all the species feed on external resources) with interspecific competition. Therefore, the purpose here is to see if large food webs with several trophic levels can be built and sustained if adaptive foraging is incorporated. large food webs with several trophic levels can be built and sustained if adaptive foraging is incorporated.

5.1 Evolutionary model

The population dynamics used here is (2.52) and the dynamics for foraging efforts is (2.33). Denoting the set of species included in level l by $S^{(l)}$, we have $B_i \subseteq S^{(l-1)}$, $R_i \subseteq S^{(l+1)}$ and $C_i \subseteq S^{(l)}$ for species i belonging to trophic level l. If i is a top predator (i.e., a species in the highest level L), R_i is empty. Species in Level 1 feed on external resources with fixed population sizes.

As a functional response $g_{ij}(t)$, we assumed the Lotka-Volterra type (2.2) (without adaptive foraging) or (2.15) (with adaptive foraging) according to Lässig et al. (2001) and Bastolla et al. (2002). But we have also investigated the stability of Holling type II (2.3) and Beddington type (2.55) without adaptive foraging.

We define the competition strength $c_{ii'}$ in equation (2.52) by potential link strength (2.51) or by effective link strength (2.53) if adaptive foraging is incorporated. We call the parameter $\sigma \leq 1$ in $c_{ii'}$ just the strength of competition from now on, even though this actually represents the ratio between the interspecific and intraspecific competition strengths.

In evolutionary food web models, the linkage patterns defined by potential connections a_{ij} change much more slowly than population sizes and foraging efforts. Therefore we can interpret the potential connections a_{ij} as a function of "evolutionary time", $a_{ij}(T)$.

To simulate the evolutionary model, we wait until the population dynamics (and foraging dynamics) reaches a fixed point (see below). Some species can become extinct due to population dynamics. Then we add a new species i' to the food web, one of whose parameters $a_{i'j}$ is slightly different (see below) from the corresponding parameter of its mother species i. The initial population size of the daughter species i' is slightly larger than the extinction threshold (twice the extinction threshold). The mother species is selected at random from all species. After this procedure, the web contains one more species. Then we simulate the population dynamics and foraging dynamics again, which could lead to extinctions of some species due to the presence of the new daughter species. This step is defined as one unit of evolutionary time T (Figure 5.1). We repeat this procedure many times and, in this way, the structure of the web (e.g., the number of species in the system, linkage patterns, number of trophic levels) changes on evolutionary time scales.

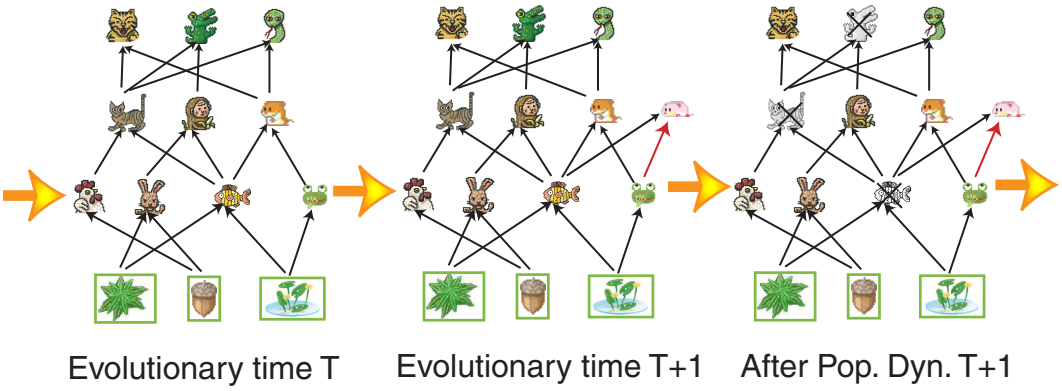


Figure 5.1: Evolutionary model.

The modification of a_{ij} to $a_{i'j}$ is done in one of the following ways:
(m-1) A prey j is selected at random from B_i, and the link strength is modified according to a rule $a_{i'j} = F(a_{ij})$ specified below.
(m-2) A new link from i' to some species p in the next lower level is created. For example if $i \in S^{(l)}$, then $p \in S^{(l-1)}$. p is chosen at random.
Each of these possible link modifications occurs with the same probability $\frac{1}{1+B_i}$, where B_i is the number of prey of i (not the prey set).

Following Bastolla et al. (2002), we expressed the connection strength a_{ij} in the form

$$a_{ij} = b_0 \frac{b_{ij}}{1 + \sum_{j' \in B_i} b_{ij'}/b_M}, \tag{5.1}$$

where b_{ij} takes an integer value in the range $[0, b_M]$. We set b_M to 10 in our simulations and b_0 to 0.2. We chose these values so that the maximal value of the connection strength a_{ij} is exactly one.

The modification of the link strength is implemented by changing the integer b_{ij} as

$$b_{i'j} = b_{ij} + \delta, \tag{5.2}$$

where δ takes the value 1 or -1 with the same probability for $j \in B_i$ (i.e., if one of the events of (m-1) occurs), or it takes the value 1 if the event (m-2) occurs. Negative $b_{i'j}$ will be set to zero. In this case the connection disappears for the new species i'. Because the connection strength a_{ij} will be saturated as a function of b_{ij} and depends on all the values of $b_{ij'}$ (but is independent of the prey population sizes), this model can be regarded as an intermediate model between Lotka-Volterra and Holling.

To understand the effects of adaptive foraging on the evolutionary model, we simulated 4 kinds of model:

1. model including classical population dynamics only,
2. model including population dynamics coupled with foraging dynamics (linear constraints $r = 1$) where competition is based on potential links a_{ij},
3. model including population dynamics coupled with foraging dynamics (linear constraints $r = 1$) where competition is based on effective links $a'_{ij} = a_{ij} f_{ij}$,
4. model including population dynamics coupled with foraging dynamics (nonlinear constraints $r > 1$) where competition is based on potential links a_{ij}.

The foraging model with nonlinear constraints and competition based on effective links has not been simulated because, for $r > 1.2$, the connection pattern defined by effective links is the same as that defined by potential links. Therefore we expect that the result will not be affected by the definition of competition in that case.

At the beginning of the simulations, we initiated the system with 7 trophic levels each of which contains 11 species. The average number of prey per species was fixed to 4 initially. Then we simulated the population dynamics with or without foraging dynamics for a sufficiently long time that the system usually reached a fixed point. If it did not reach a fixed point during a predetermined time, we

stopped the dynamics at the end of this time period. When the population size of a species dropped below the extinction threshold during the evaluation of the dynamics, the species was regarded as extinct and removed from the system. The extinction threshold was set to 10^{-3} in our simulations. After running the dynamics, a mutant species was introduced into the web, giving rise to a new food web. The introduction of the daughter species is specified by the evolutionary rules described above. Again, we simulated the dynamics of this new system. This set of procedures is defined as one evolutionary time step ($T \to T + 1$). We included 4 external resources. It is possible to take only one external resource. But in this case we found that, due to strong competition, we need a resource with a size larger than 4 times the size of a single resource in the case of 4 resources to obtain the same complexity of webs (i.e., the same number of trophic levels) in the end. We also found that the simulation becomes much slower if we enlarge the size of resources. Therefore we put several resources in level 0. The simulation becomes much slower if we enlarge the size of resources, so we put several resources in Level 0. The mortality and intraspecific competition are fixed to $\alpha_i = 0.02, \beta_{ii} = 0.2$. For the ecological efficiency λ_{ij} we choose an ecologically meaningful value 0.15 (Krebs, 2002). For the adaptive dynamics we set $\kappa = 2$.

In the next section, we show the outcome of the simulations at a fixed evolutionary time $T = 1500$ as a function of the resource size R and of the interspecific competition strength σ. Our purpose is to compare the results of models with or without adaptive foraging and also to understand the effect of the competition strength σ in the model with foraging dynamics. In section 5.3 we will then discuss the long-term evolution of model webs and analyze the properties of the time series.

5.2 Food web structure at T=1500

We evaluated the system size and trophic level structure of webs with and without foraging dynamics at the evolutionary time $T = 1500$, as function of the parameters R (resource size) and σ (competition strength). We simulated 200 samples for the model without foraging dynamics and 100 samples for the model with foraging dynamics for each set of parameters $R = 10, 20, 50, 100, 200; \sigma = 0.9, 0.95, 1.0$, and we averaged over the samples. Figure 5.2 shows the number of species (i.e., the system size) and Figure 5.3 shows the average trophic level (Av.Tro.Lv.) and the average maximum trophic level (Max.Tro.Lv.) for all these situations. The constraint for the foraging dynamics is linear. In these figures, the competition terms are based on potential links, thus these data allow a comparison between model 1. and model 2. mentioned in the last section. We notice that the system may not yet be in a stationary state at this evolutionary time point. The maximum trophic level is identical to the chain length (distance) from the resources to the top predators. For example, the food web depicted in Figure 5.5 has the maximum trophic level 3. The maximum trophic level can be occupied by any number of species, a network with only one top predator has therefore the same maximum level. The average trophic level is the trophic level a species belongs to on average. It is defined by $\sum_{l=1}^{L} lS^{(l)} / \sum_{l=1}^{L} S^{(l)}$, where L is the maximum trophic level and

$S^{(l)}$ is the number of species in level l. This quantity depends on the distribution of species, and the two food webs shown in Figure 5.5 and 5.6 have a different average trophic level, while they have the same maximum trophic level. It can happen in principle that a food web has a low average trophic level even if the maximum trophic level is large.

Figure 5.4 compares the species number and the average and maximum trophic level for models with foraging dynamics with linear and nonlinear ($r = 2$) constraints for fixed $\sigma = 1.0$.

We can discern the following features of the data:
(1) From Figure 5.2, we conclude that the model with foraging dynamics leads to much larger webs than the model without foraging dynamics. Especially at $\sigma = 1.0$, the model without foraging dynamics results in extremely small systems. But if foraging dynamics is added to the model, even at $\sigma = 1.0$ the resulting webs are large enough that they deserve to be called a web.

We notice that the energy flow $\sum_i a_{i0}E$ from the external resource of size E into the webs without foraging tends to be larger than the energy flow $\sum_i a_{i0}f_{i0}E$ into the webs with adaptive foraging. (The index 0 in the couplings and efforts denotes the external resource). Moreover, the fixed point condition of the dynamics with adaptive foraging requires $a_{i0_1}E_1 = a_{i0_2}E_2$ for every pair of external resources used by a species, which means in practice that a species can only feed on one external resource at a time, because the couplings and resource sizes are fixed quantities and cannot be adjusted to satisfy this equality.

We have also simulated the model with efforts but without adaptation, i.e., the connection strength a_{ij} is divided by the number of i's prey, that is $f_{ij} = 1/B_i$. In this model, the average energy flow from external resource must be same as the foraging model as is discussed in chapter 3. However, we found that this model is so unstable in the investigated parameter regime that a collapse occurs at an early stage of the evolution, and the system contains only 2 or 3 species thereafter.

(2) Figure 5.3 shows that the model with foraging dynamics leads to larger maximum trophic levels than without foraging dynamics, except for the case $\sigma = 1$. At $\sigma = 1$, a system without adaptive foraging has only 4 species. By looking at the individual data, we found that these four species feed either directly on the four external resources ($S^{(1)} = 4$), or that three of them form a food chain ($S^{(1)} = 2, S^{(2)} = 1, S^{(3)} = 1$). For small resources, the first case is more frequent, for larger resources, the second situation appears more often. Once the food chain structure is obtained, it will be retained, and the system has a high maximum trophic level. For the model with foraging dynamics, we find nontrivial webs already for the parameter values $R = 10, \sigma = 1$. There are always 2 trophic levels each of which contains many species.

The value of the competition strength does not affect the average trophic level ((b), (d)). This means that a smaller competition strength does not lead to higher trophic levels. The interspecific competition affects only the "lateral" direction, i.e., with weaker competition the number of species in each level becomes larger.

This effect becomes even more pronounced when the competition term is based on effective connections a'_{ij} (model 3.). As was mentioned in chapter 2, this model

leads to competition avoidance behavior (or niche segregation), with species of the same trophic level assigning their efforts to different prey. Therefore, the competition in this system is in general smaller than when competition is based on potential connections. For instance, for the parameter value $\sigma = 1, R = 10$, the average trophic level is 1.4, and the average system size is 122.8. In Figure 5.7, we show an example of a web generated by the model with competition avoidance effect. Only for this model, the resource size R is chosen smaller and the interspecific competition strength σ is chosen larger than in other models for the reason of computational power. We need much more computational power to simulate this model than other models with the same parameter values, because the resulting food webs are much larger.

(3) Comparing systems with linear and nonlinear constraints on the foraging effort (Figure 5.4), one finds that the network size is larger with nonlinear constraints (a), but that the maximum and average trophic levels are similar in both cases ((b) and (c)). This fact confirms our earlier finding that competition does not play an important role at determining trophic levels. The total energy flow from the resources into a web with linear constraints must be smaller than with nonlinear constraints, because the number of effective links (i.e., the links that actually carry energy) is much smaller than the number of potential links with linear constraints. In contrast, with nonlinear constraints the number of effective links is equal to the number of potential links since all efforts are nonzero, even though they may be very small. Although they carry no energy, inactive links in networks with linear constraints contribute to the competition term, and therefore the relative effect of the competition is larger in webs with linear constraints than with nonlinear constraints. This is why the model with the nonlinear constraints generates larger webs than the linear case. We already saw above that in the case of linear constraints the system size becomes larger if the competition term is based on effective links.

(4) From Figures 5.5-5.8, we can deduce more properties of the different models. These figures show typical food webs at $T = 1500$ with the parameters $R = 200$ and $\sigma = 0.9$ (Figures 5.5, 5.6 and 5.8), and $R = 10$ and $\sigma = 1.0$ (Figure 5.7). Resources are indicated as green squares. Figure 5.5 shows a food web generated by the model with population dynamics only, and Figure 5.6 shows a food web generated by including foraging dynamics (with linear constraints), with competition based on potential connections; the two parts of the figure show a link for each nonzero potential connection (a) and for each nonzero effective connection (b). Figure 5.7 shows a food web for a model where competition is based on effective links. Shown are nonzero effective links. (The reason for the different parameter values for this model is the computational power). Figure 5.8 shows a food web obtained by applying foraging dynamics with nonlinear constraints, with the value $r = 1.05$. For a value r so close to 1, there are many very weak links. Only effective links with $a'_{ij} > 10^{-4}$ are shown in this figure.

From these figures we conclude that species in a web generated by foraging (linear constraints) can be grouped according to what potential prey they have.

For example, the species in trophic level 3 in Figure 5.6 (a) can be clearly classified into 2 groups and the species in level 2 can be classified into 4 groups. Group 4 consists of species that do not belong to the first three large groups. By comparing figures (a) and (b), we see in Level 2 that even when species have the same potential prey, they can have different effective prey. This means that competition is reduced by foraging dynamics, even though there is no clear niche segregation effect, as discussed in 2.1.5.

The different models differ also in the pattern of links to the resources. While Level-1 species in models without foraging dynamics (model 1.) have several (potential) links to the resources (Figure 5.5), there is only one potential link for each species in Level 1 when foraging dynamics is included (model 2. Figure 5.6 (a)). Actually, we found that all webs generated by models that include adaptive foraging will eventually have only one link to the external resources for each species in Level 1. This is because a species having more than one potential link to the resources is nevertheless only allowed to have one effective link to the resources, but it has more competition due to the inactivated links than a species with only one potential link to the resources. Therefore it is better for the species that inactivated links do not exist at all if competition is based on potential connections.

We can analyze this phenomenon by considering the situation illustrated in Figure 5.9. There are two groups of species with one potential link to the resources; one species (the one with the index 0) has two potential links of strength a_0 and xa_0 with $x < 1$. Because of $xa_0 < a_0$, species 0 feeds on only the first resource at a fixed point of the adaptive dynamics. In the following, we estimate the population size N_0 of species 0 at a fixed point. The competition terms based on potential connections for each group are according to Equation (2.50) expressed by

$$c_{0m}^{(0,1)} = \sigma\beta \frac{a_0 a_m^{(1)}}{\sqrt{a_0^2 + x^2 a_0^2}\sqrt{a_m^{(1)} a_m^{(1)}}} = \sigma\beta \frac{1}{\sqrt{1+x^2}} \tag{5.3}$$

$$c_{0n}^{(0,2)} = \sigma\beta \frac{x a_0 a_n^{(2)}}{\sqrt{a_0^2 + x^2 a_0^2}\sqrt{a_n^{(2)} a_n^{(2)}}} = \sigma\beta \frac{x}{\sqrt{1+x^2}} \tag{5.4}$$

$$c_{mm'}^{(1,1)} = c_{nn'}^{(2,2)} = \sigma\beta \quad (m \neq m' \text{and } n \neq n') \tag{5.5}$$

$$c_{mn'}^{(1,2)} = c_{m'n}^{2,1} = 0. \tag{5.6}$$

Here the superscripts indicate groups. For example, $a_m^{(1)}$ is the connection strength to the resource of species m in group 1. In the following, we will omit the superscripts, and we will always use index m for group 1 and index n for group 2 and index 0 for species 0, which has potential links to both resources. We consider only the case where all the species are surviving ($N > 0$). Then the fixed point equation

is given by setting the growth rates to zero:

$$E_0' - \beta N_0 - \sigma\beta \frac{1}{\sqrt{1+x^2}} \sum_{m=1}^{S_1} N_m - \sigma\beta \frac{x}{\sqrt{1+x^2}} \sum_{n=1}^{S_2} N_n = 0, \tag{5.7}$$

$$E_m - \beta N_m - \sigma\beta \sum_{\substack{m'=1 \\ m' \neq m}}^{S_1} N_{m'} - \sigma\beta \frac{1}{\sqrt{1+x^2}} N_0 = 0, \tag{5.8}$$

$$E_n - \beta N_n - \sigma\beta \sum_{\substack{n'=1 \\ n' \neq n}}^{S_2} N_{n'} - \sigma\beta \frac{x}{\sqrt{1+x^2}} N_0 = 0. \tag{5.9}$$

E_m is defined by $E_m = a_m R - P_m - \alpha$. $a_m R$ is the energy inflow from the resources, $P_m = \sum_{k \in R_m} a_{km} N_k$ is the energy loss by predation, and α is the mortality. E_n is defined in the same way. The "effective" energy inflow to species 0 is $E_0' = E_0 + x a_0 R d$ with $E_0 = a_0 R - P_0 - \alpha$; $x a_0 R d$ is the energy inflow from the second resource. The parameter d has the value $d = 1$ for the model with population dynamics only, and $d = 0$ for the model with foraging dynamics (linear constraints), because even though species 0 has a potential link to the second resource, the species actually feeds only on the first resource due to the fixed point condition of the foraging dynamics with linear constraints. We notice that E_0 does not contain the parameter x.

We will now evaluate the population size N_0 as a function of the parameters $x, a_0, a_m, a_n, \sigma, \beta, P_0, P_m, P_n, R, S_1$, and S_2. If there were no interspecific competition ($\sigma = 0$), and no connection to the second resource ($x = 0$), the population size N_0 would be just proportional to E_0, i.e., $N_0 = E_0/\beta$. Due to the interspecific competition, however, the actual population size is smaller than E_0/β as long as all the other population sizes N_m and N_n are positive. Now the question is how the relative connection strength x to the second resource affects the population size N_0.

By summing Eq. (5.8) and Eq. (5.9) over $m = 1, \cdots, S_1$ and $n = 1, \cdots, S_2$ respectively, we find the expressions

$$\sum_{m=1}^{S_1} N_m = \frac{\sum_{m=1}^{S_1} E_m - \sigma\beta S_1 N_0/\sqrt{1+x^2}}{(\sigma S_1 + (1-\sigma))\beta}, \tag{5.10}$$

$$\sum_{n=1}^{S_2} N_n = \frac{\sum_{n=1}^{S_2} E_n - x\sigma\beta S_2 N_0/\sqrt{1+x^2}}{(\sigma S_2 + (1-\sigma))\beta}. \tag{5.11}$$

Now we introduce new variables y and z that are defined as the relative difference between the effective energy inflow $E_0 = a_0 R - P_0 - \alpha$ to species 0 and the average "effective" energy inflow to the species of the two groups, $\sum_{m=1}^{S_1} E_m/S_1$ and $\sum_{n=1}^{S_2} E_n/S_2$ by

$$y = \frac{E_0 - \sum_{m=1}^{S_1} E_m/S_1}{E_0}, \tag{5.12}$$

$$z = \frac{E_0 - \sum_{n=1}^{S_2} E_n/S_2}{E_0}. \tag{5.13}$$

The variables y and z are functions of the connection strengths (a_0, a_m, a_n) and of the energy loss by predation P_0, P_m, P_n, but these variables do not include x. For example, $y = 0.05$ means that the average effective energy inflow into group 1 is 5 % smaller than E_0 at the fixed point: $\sum_{m=1}^{S_1} E_m/S_1 = 0.95 \times E_0$.

Using these variables y and z, we substitute the expressions (5.10) and (5.11) into (5.7) to get the expression for N_0:

$$E_0 + xa_0Rd - \beta N_0 - \sigma\frac{S_1(1-y)E_0 - \sigma\beta S_1 N_0/\sqrt{1+x^2}}{\sqrt{1+x^2}(\sigma S_1 + (1-\sigma))} - \sigma x\frac{S_2(1-z)E_0 - x\sigma\beta S_2 N_0/\sqrt{1+x^2}}{\sqrt{1+x^2}(\sigma S_2 + (1-\sigma))} = 0. \quad (5.14)$$

We notice that in this equation all the information about the connection pattern and the population sizes of predators (a_m, a_n, P_m, P_n) is absorbed into the variables y and z.

Solving this equation with respect to N_0, we have

$$N_0 = \frac{1-f(x)}{1-g(x)} \cdot \frac{E_0}{\beta} + \frac{x}{1-g(x)} \cdot \frac{a_0Rd}{\beta}, \quad (5.15)$$

with

$$f(x) = \frac{\sigma S_1(1-y)}{\sqrt{1+x^2}(S_1\sigma + (1-\sigma))} + \frac{x\sigma S_2(1-z)}{\sqrt{1+x^2}(S_2\sigma + (1-\sigma))}, \quad (5.16)$$

$$g(x) = \frac{\sigma^2 S_1}{(1+x^2)(S_1\sigma + (1-\sigma))} + \frac{x^2\sigma^2 S_2}{(1+x^2)(S_2\sigma + (1-\sigma))}. \quad (5.17)$$

Now we denote the ratio between a_0Rd and E_0 by D:

$$D = \frac{a_0Rd}{E_0}. \quad (5.18)$$

For the model with population dynamics only, D is larger than 1 because $E_0 = a_0R - P_0 - \alpha < a_0R$, and for the model with foraging dynamics, we have $D = 0$. We then find the final expression for N_0:

$$N_0 = h(x) \cdot \frac{E_0}{\beta}, \quad (5.19)$$

where

$$h(x) = \frac{1-f(x)}{1-g(x)} + \frac{x}{1-g(x)} \cdot D. \quad (5.20)$$

We plot this function in Figure 5.10. Increasing y and z just shifts the curves upwards, but does not change the trend of the curve. Thus the important parameter is σ. The population dynamics with and without foraging dynamics are leading to opposite results. For a species without adaptive foraging, having a stronger connection to the second resource is always better since the benefit of the additional

link is larger than the cost of competition. In contrast to this, a species doing adaptive foraging can hardly survive if the species has a strong potential link to the second resource. According to the simulation results of the evolutionary model, the best situation for the species in level 1 is achieved already at $T = 1500$ in the model with foraging dynamics, where each species has only one potential link to the resources.

We can expect that increasing the nonlinearity r moves the curves $h(x)$ of the model with foraging dynamics closer to the ones without foraging dynamics, because the effect of foraging dynamics becomes smaller for $r \to \infty$ (Chapter 2 and 3). For $r = 2$, the function $h(x)$ must be a decreasing function because we found that even in this case a species in level 1 has only one potential link (not shown). If competition is based on effective links, it is not important at a fixed point how many potential links a species has to resources, because the inactivated links do not contribute to the competition. According to our simulations, there exist several species that have more than one potential link to the resources, but most species have only one potential link to the resources.

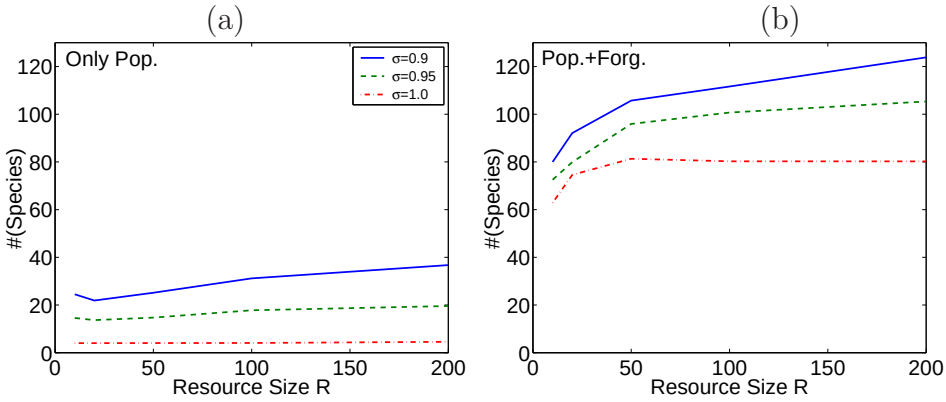


Figure 5.2: Average number of species at $T = 1500$ for (a): population dynamics without adaptive foraging, and (b): population dynamics with adaptive foraging as a function of resource size R and competition strength σ. The averages are taken over 200 samples for (a) and 100 samples for (b).

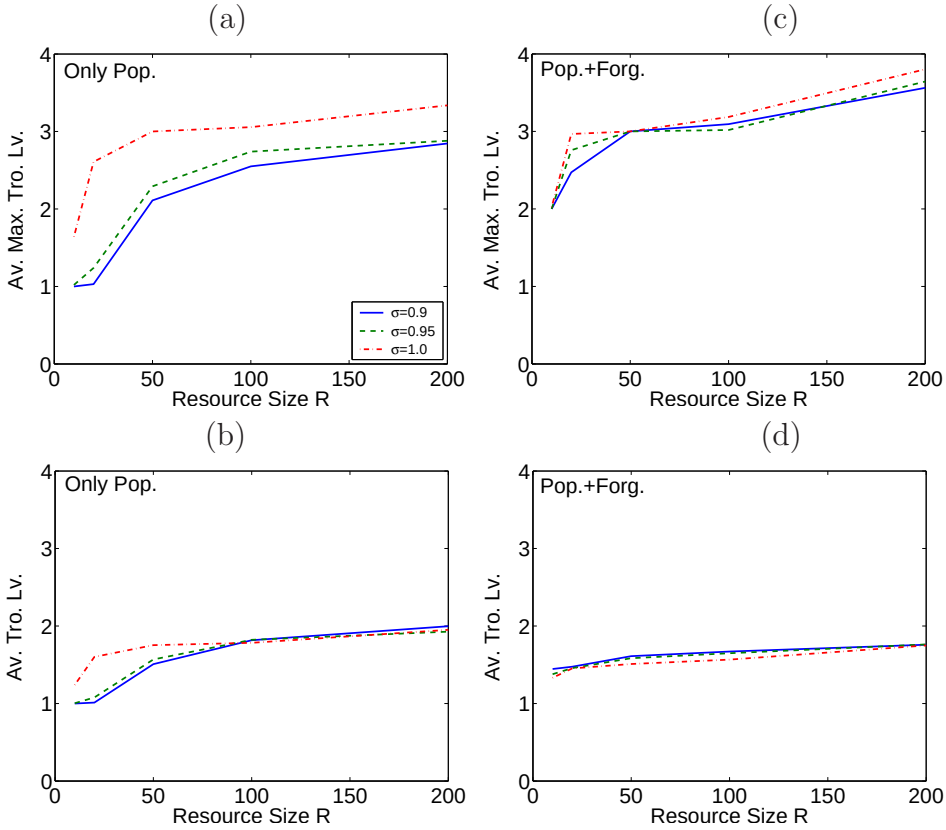


Figure 5.3: Average maximum trophic level ((a) and (c)) and average trophic level ((b) and (d)) at $T = 1500$, without ((a) and (b)) and with ((c) and (d)) adaptive foraging. The maximum trophic level is identical to the shortest chain length from the resources to the top predators.

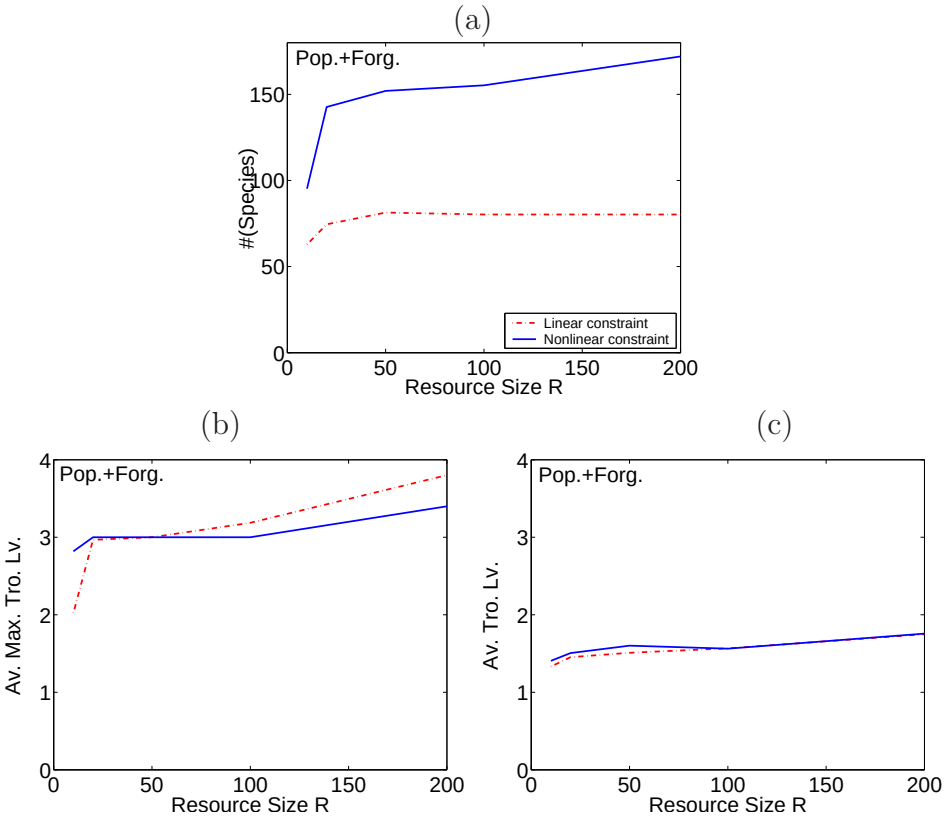


Figure 5.4: (a) number of species (b) Average maximum trophic level (c) average trophic level at $T = 1500$ for models with linear constraints on foraging efforts (dashed line) and nonlinear constraints ($r = 2$, solid line).

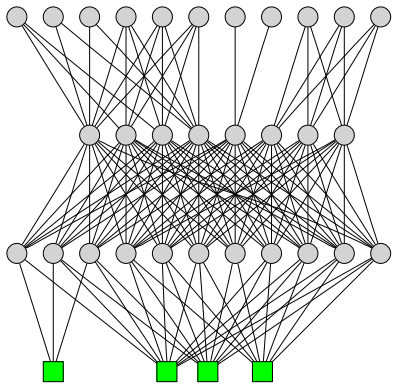


Figure 5.5: Example of a foodweb at $T = 1500$ for population dynamics only (model 1.). The parameters are $R = 200$ and $\sigma = 0.9$.

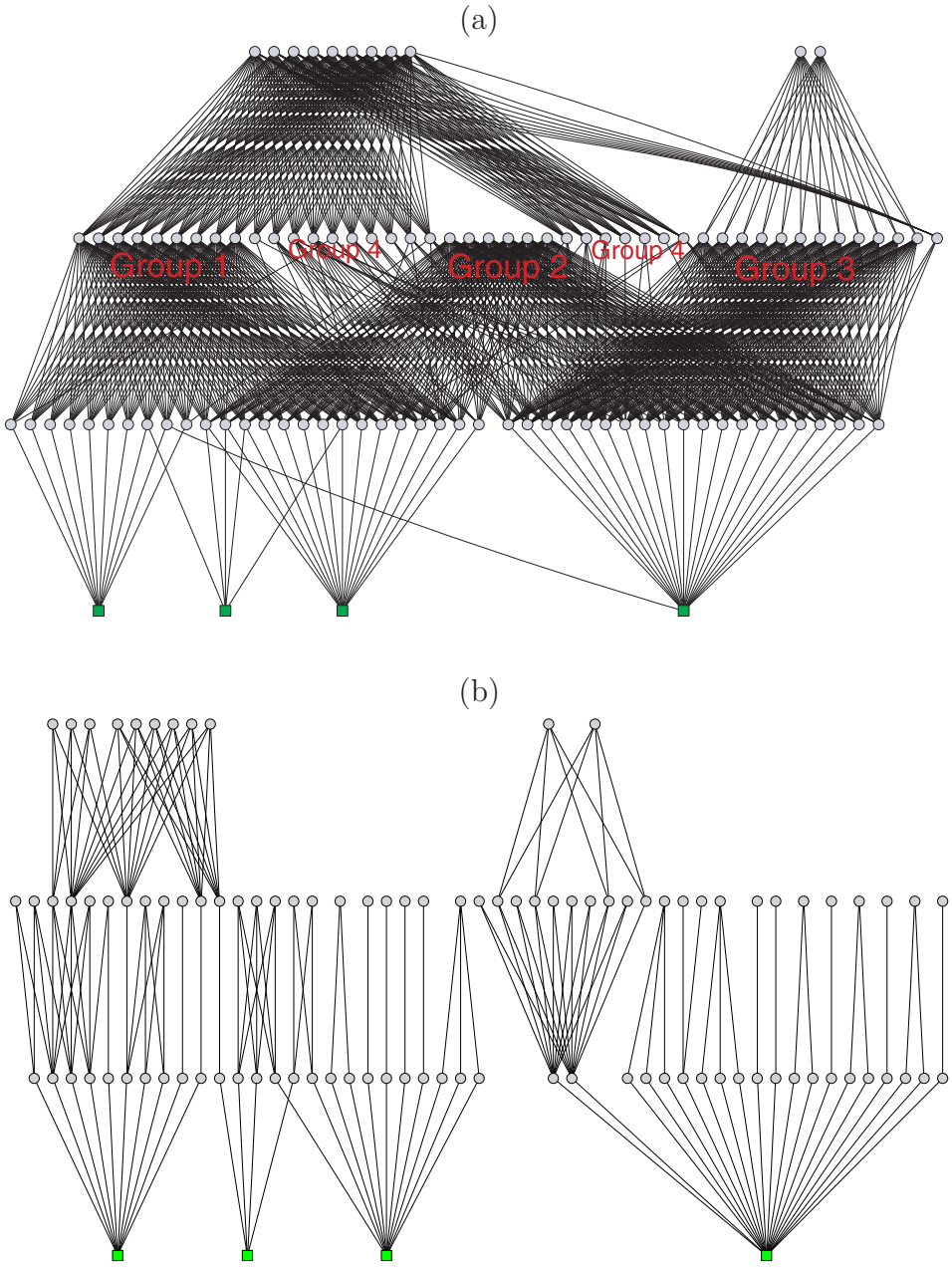


Figure 5.6: Example of a foodweb at $T = 1500$ for a model with adaptive foraging (linear constraints, model 2.). Shown are nonzero potential links (a) and nonzero effective links (b). The parameters are again $R = 200$ and $\sigma = 0.9$.

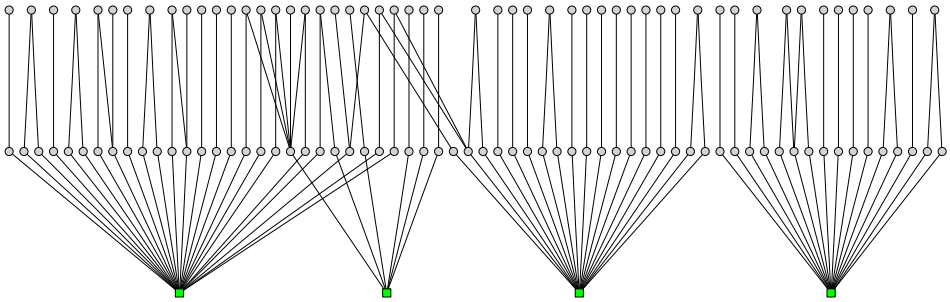


Figure 5.7: Example of a foodweb at $T = 1500$ for a model with adaptive foraging (linear constraints), with competition based on effective links a'_{ij}, model 3.). Shown are nonzero effective links. The parameters are $R = 10$ and $\sigma = 1$.

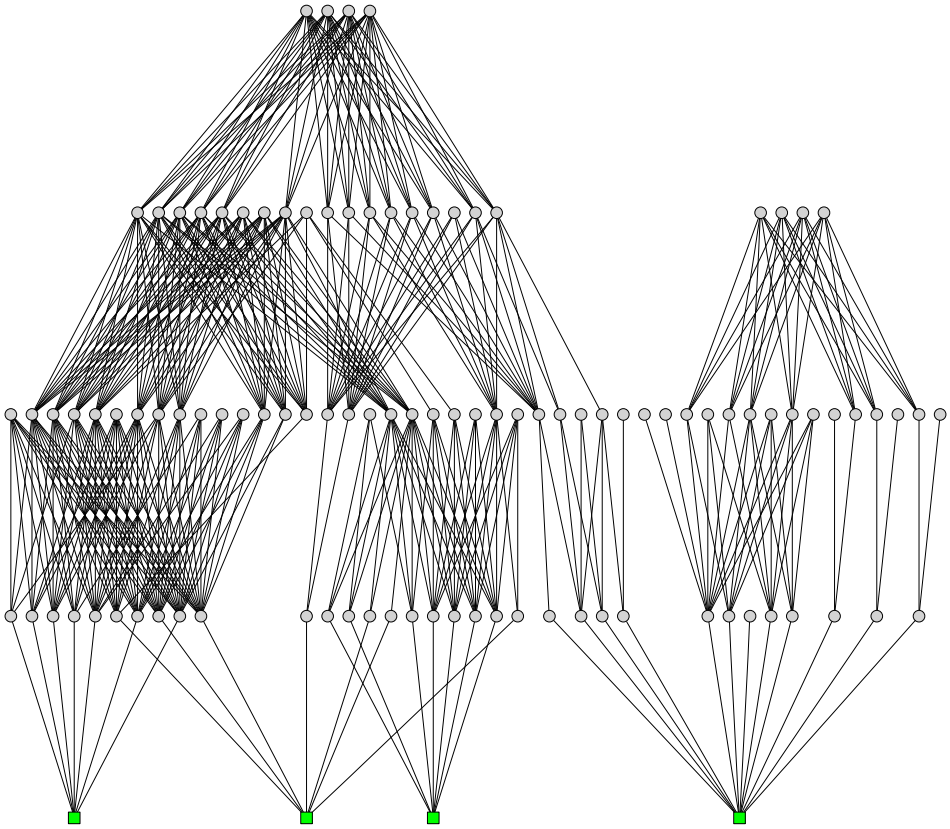


Figure 5.8: Example of a foodweb at $T = 1500$ with adaptive foraging (nonlinear constraints, $r = 1.05$, model 4.) Shown are nonzero effective links. The parameters are $R = 200$ and $\sigma = 0.9$.

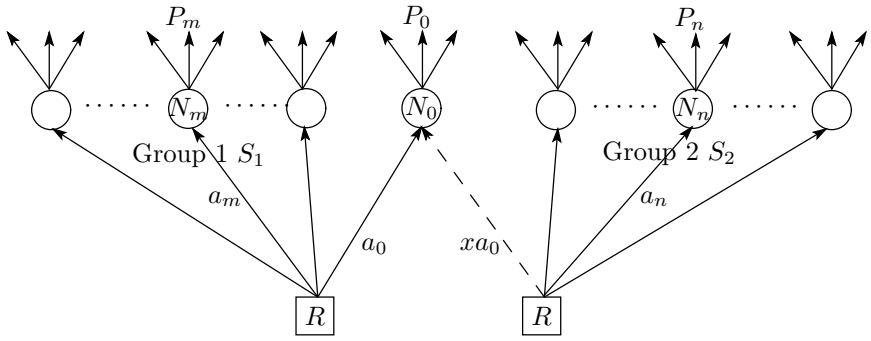


Figure 5.9: Situation considered in the analytical calculation.

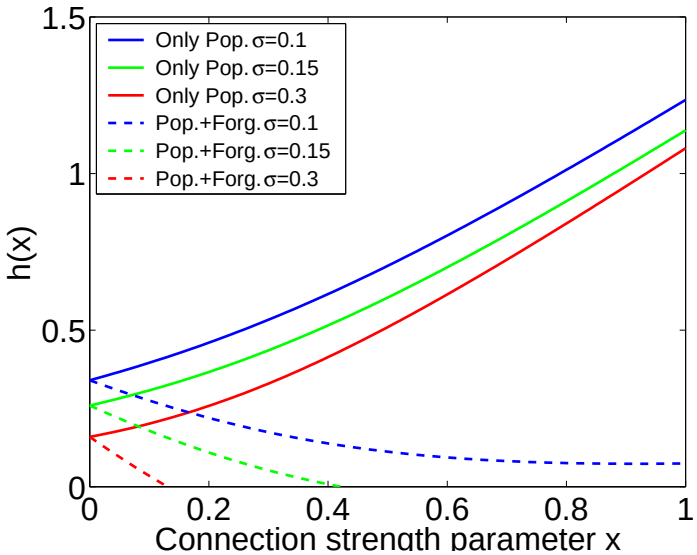


Figure 5.10: Ratio $h(x) = E_0/\beta N_1$ as a function of the relative connection strength x of species 0 to the second resource (see previous figure). The system parameters are $S_1 = 20, S_2 = 15, y = z = 0$. For the model without adaptive foraging, it is $D = 1.1$.

5.3 Long time series

Now we study longer time series of the network evolution in order to understand the long-term properties of the models. We plotted in Figures 5.11 (model 1., no adaptive foraging) and 5.13 (model 2: adaptive foraging with linear constraints) the time series of the number of species $S(T)$ (a) and of the average trophic level $\sum_{l=1}^{L} lS^{(l)} / \sum_{l=1}^{L} S^{(l)}$ (b) for the parameter values $R = 200$ and $\sigma = 0.9$. We see in Figure 5.11 (a) a collapse of all the higher trophic levels around $T = 10700$. After the collapse of higher trophicl levels, there is of course only one trophic level i.e., all the species feed on external resources. In Figure 5.13, there is no such collapse even though there are large extinction events; higher trophic levels are retained even after a long time. Actually Figure 5.13 (b) shows stationary behavior. The

fluctuations appear to be smaller than those in Figure 5.11 (b). This indicates that there exist essential differences between the models.

To understand these differences, we plotted the time series of the species number and of the average trophic level together in Figures 5.12 (a) and 5.14 (a). One can see in Figure 5.14 (a) (Without foraging dynamics) that the average trophic level becomes smaller at a large extinction event. This mean that extinction events affect primarily species in higher trophic levels. Indeed, there is a positive correlation between species number and average trophic level (Figure 5.12 (b)). Contrary to this, we do not find such clear correlations in the model with adaptive foraging. In Figure 5.14 (a), at the extinction event at time $T = 34600$, we see a positive correlation, but at the extinction event at time $T = 36500$, we see no such correlation. Neither can a correlation be seen in Figure 5.14 (b). This difference will be discussed again later.

Figure 5.15 shows (a) the size distribution of extinction avalanches and (b) the probability distribution for robustness values smaller than 1. The data are taken from the time series shown in Figure 5.11 and Figure 5.13. The large points at a robustness value of 1 in Figure 5.15 are the probability that no species becomes extinct during an evolutionary time step. The avalanche size is defined as $S(T) - S(T+1) > 0$ for each evolutionary time T. The robustness is defined as $S(T+1)/(S(T)+1)$, with $S(T)+1$ being the number of species immediately after introduction of the daughter species and before the evaluation of the population dynamics at $T+1$. In Figure 5.15 (a), we do not see a qualitative difference between the cases with and without foraging dynamics. Both have scale free distributions. The exponent for the model without foraging is smaller than that of the model with foraging dynamics. This means that large extinction events are more likely in the model without foraging dynamics. Figure 5.15 (b) shows a clear difference between the two models. The model with foraging has a larger weight at high robustness values, while the model without foraging shows a maximum at intermediate robustness values and has a small weight at large robustness (or small extinction events). This means that in the model without foraging dynamics, if a species becomes extinct, other species are also likely to become extinct at once. This fits together with Figure 5.16 (a) where the number of species and the average competition are plotted together. If there are similar species, average competition must be large. We see that at large extinction events the average competition is reduced. This means that many similar species become extinct, due to losing a common main prey.

Figure 5.17 shows other examples of the model without foraging dynamics. (a) is an example with another parameter set $R = 1000, \alpha = 1, \beta = 1$ and $\sigma = 0.8$. (b) and (c) are obtained with Holling type II functional response. In this case, we defined the connection strength by

$$a_{ij} = \log b_{ij}, \tag{5.21}$$

where $b_{ij} > 1$. The logarithm was taken in order to prevent the connection strength from increasing without limits. We defined the dissimilarity $\bar{\rho}_{ii'}$ between two species

by comparing their feeding patterns,

$$\bar{\rho}_{ii'} = \frac{\sum_{j=1}^{S^{(l-1)}} \rho_i^j \bigoplus \rho_{i'}^j}{S^{(l-1)}}, \tag{5.22}$$

where ρ_i^k takes the value 1 if i is a predator of j and 0 otherwise, and $\bigoplus$ is XOR. The term $\sum_{j=1}^{S^{(l-1)}} \rho_i^j \bigoplus \rho_{i'}^j$ represents the hamming distance between the two species. Then we took an average of $\bar{\rho}_{ii'}$ over all pairs of species in the same level.

The figures show that the number of species and the average competition (average dissimilarity) are correlated (anticorelated). Especially, at the time points where large extinction events occur, the competition (the dissimilarity) suddenly decreases (increases).

This means that the population dynamics does not favor a species that is in some respect "better" than others. Instead if we introduce a new similar species into a web, all the species are possibly alive. However due to the competition, the population size must become smaller in general, and the species have similar population sizes because they have similar prey sets. Once the population sizes of the species have decreased below the extinction threshold, all the species become extinct. We have seen that a similar phenomenon happens for the Beddington functional response, even though competition is implemented in a different way, i.e., there is no separate term for energy loss due to competition, but competition influences the amount of food that is taken. In Figure 5.16 (b), which is for a model with adaptive foraging, we have a different result. (We show here the data of level 2 because they are most clear. But similar phenomena occur in higher levels.) This can be in general understood because species with foraging dynamics can reduce competition by flexibly choosing their prey. If two similar predators feed on the same prey, the population size of the prey is in general smaller. Once the prey population becomes so small that the predators cannot live on it any more, one of them can switch to other prey. In this way the species reduce competition.

The increase of competition after a large extinction event can be understood by the following argument. As was shown in Figure 5.6, species form groups that have similar potential prey. If the species in a group become extinct at the same time (this must happen in large extinction avalanches), the average competition in the next higher trophic level increases.

The above two arguments support the result shown in Figure 5.14. Top predators feed on species from different groups. Even if a group gets lost from a web, this affects only some top predators, and their trophic level is not at the risk of extinction.

5.4 Conclusion

We have shown that model food webs with population dynamics only are unstable under evolution regardless of the functional response used if competition is incorporated. This result is similar to what was reported in Drossel et al. (2004) even though the authors used a different evolutionary model. They found further that large food webs can be built by introducing a mechanism that makes it possible for a

predator to focus on those prey which the predator is best adapted to. The simplest way which the authors chose to implement adaptation was to replace the connection strength a_{ij} by the effective connection strength $a'_{ij} = a_j^{\max}(1-(a_j^{\max}-a_{ij})/\delta)$, with δ being a small parameter and $a_j^{\max}$ being the largest connection strength among all links to j. Negative a'_{ij} will be set to zero, i.e., $a_{ij} \leq a_j^{\max} - \delta$ means $a'_{ij} = 0$. Therefore the number of species a predator actually feeds on is limited. This artificial and simple method produces large webs.

In this chapter we found, based on the model proposed in Lässig et al. (2001) and Bastolla et al. (2002), that large webs can be sustained if each predator eventually concentrates on feeding on those prey which offer the maximum potential payoffs $a_{ij}N_j$ (adaptive foraging with linear constraints). But moreover we have shown that complex webs will be still built when nonlinear constraints are used. In this case, the number of effective prey of a predator is not limited but each predator adjusts its effective connection strengths so that the growth rate is maximized.

In Lässig et al. (2001), the authors argued using a mean-field approximation that their evolutionary model without adaptive foraging must produce food webs the structure of which is similar to realistic food webs. For example, the number of species at level l increases with l for lower levels and decreases again for higher l, i.e., the number of species is large at intermediate levels. However, these authors did not show that such features can emerge in a computer simulation of the model. By performing such computer simuations, we found that the model without adaptive foraging is unstable anyway, and that the above-mentioned structure cannot be obtained even if adaptive foraging is incorporated. The number of species always decreases as l increases (for both linear and nonlinear constraints). To conclude, we have shown that by including adaptive foraging into the model by Lässig et al. (2001) and Bastolla et al. (2002), a compex foodwebs structure with several trophic levels can be maintained over long evolutionary times. However, the details of the foodweb structure do not agree with real webs. We may need another mechanism to obtain more realistic food webs.

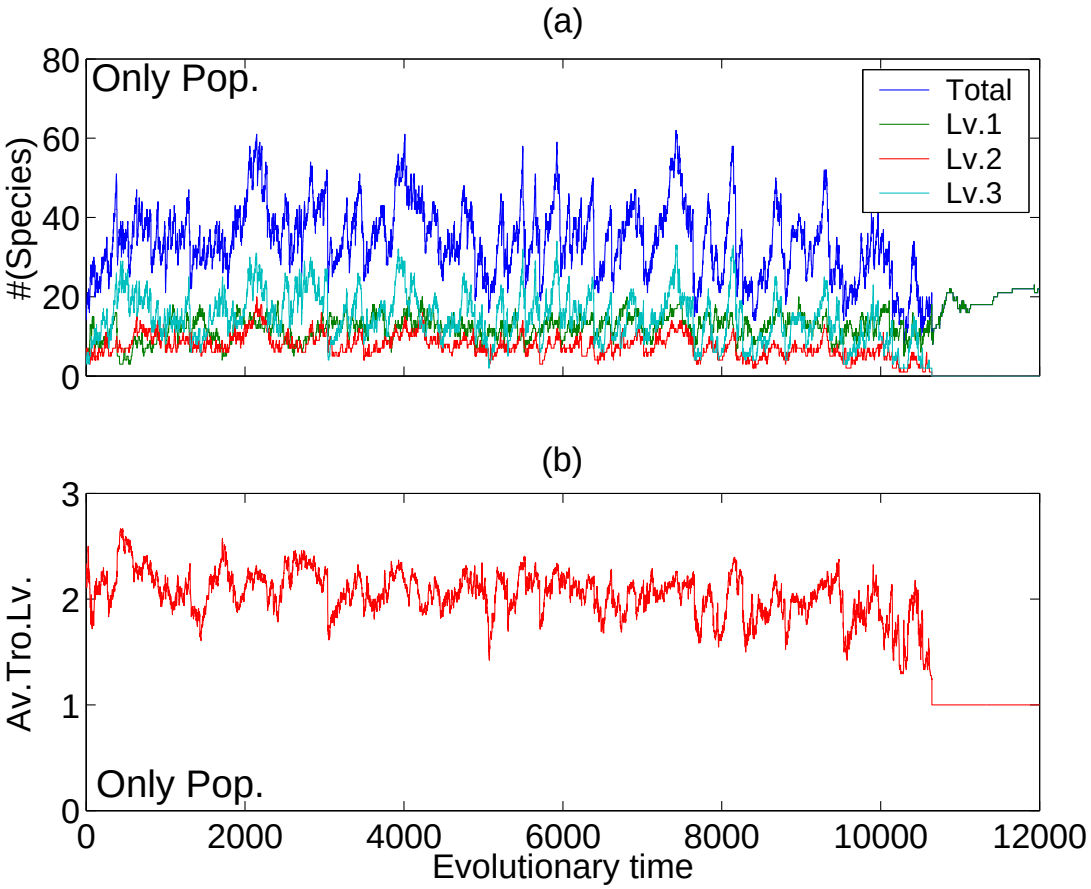


Figure 5.11: A time series for (a) the number of species and (b) the average trophic level for the model without adaptive foraging, with the parameter values $R = 200$ (resource size) and $\sigma = 0.9$ (competition strength).

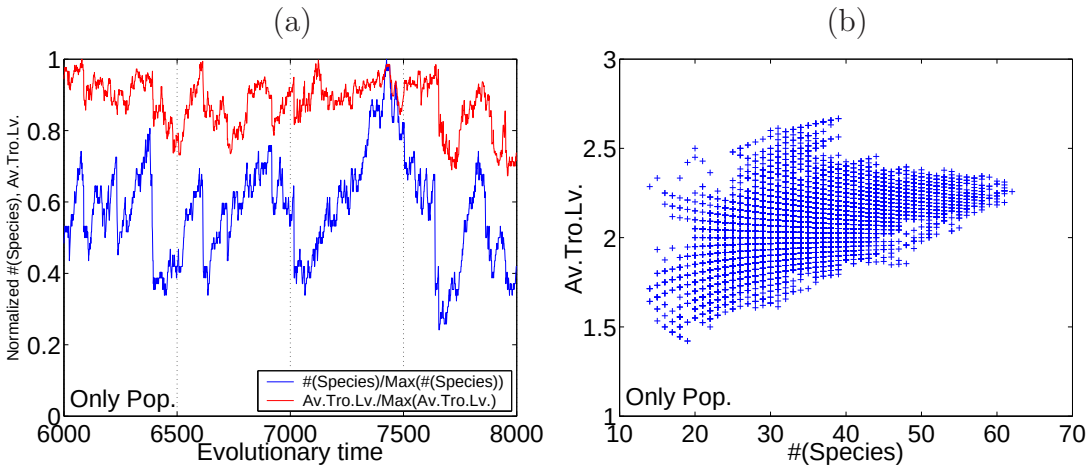


Figure 5.12: (a): Zoom into Figure 5.11. Species number and average trophic level are now plotted in the same graph. (b): Correlation between species number and average trophic level.

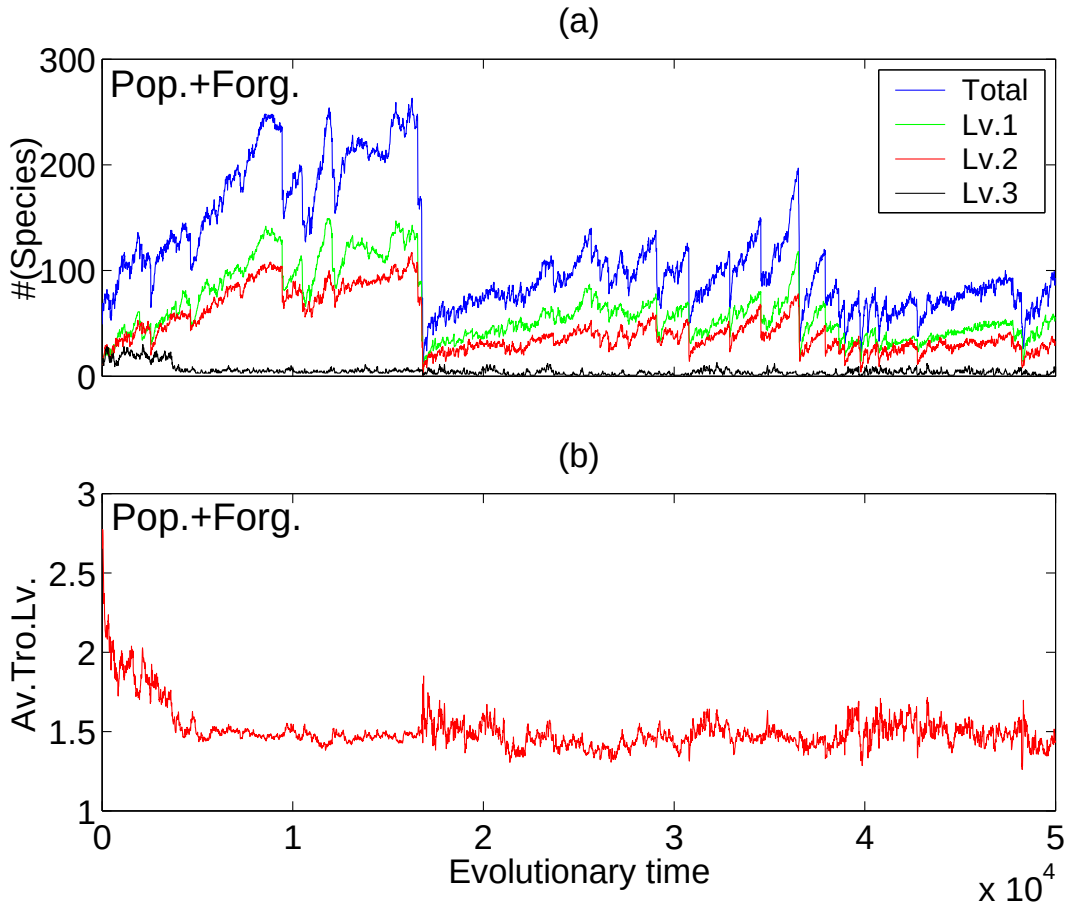


Figure 5.13: A time series for (a) the number of species and (b) the average trophic level for the model with adaptive foraging, with the parameter values $R = 200$ (resource size) and $\sigma = 0.9$ (competition strength).

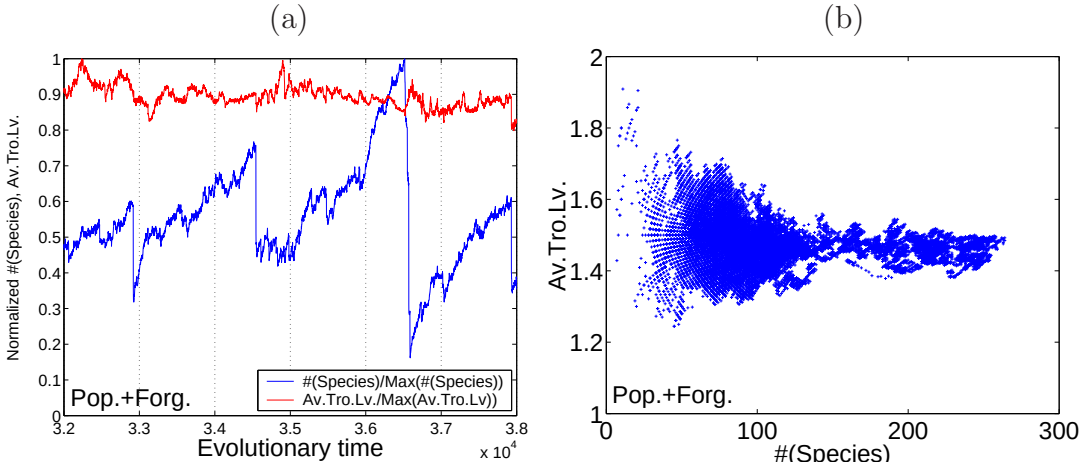


Figure 5.14: (a): Zoom into Figure 5.13. Species number and average trophic level are now plotted in the same graph. (b): Correlation between species number and average trophic level.

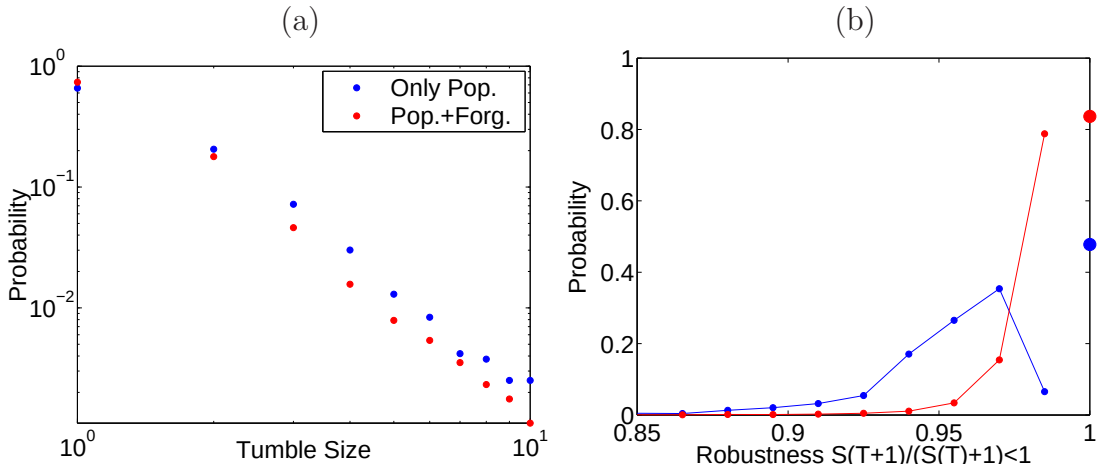


Figure 5.15: Distribution of (a) avalanche (or tumble) size and (b) robustness valies obtained from Figures 5.11 and 5.13. The avalanche size was obtained by counting $S(T) - S(T+1) > 0$ at each evolutionary time step T. The robustness was obtained by calculating $S(T+1)/(S(T)+1)$ at each time step. $S(T)+1$ is the number of species immediately after addition of the daughter species, and before the evaluation of the population dynamics at $T+1$.

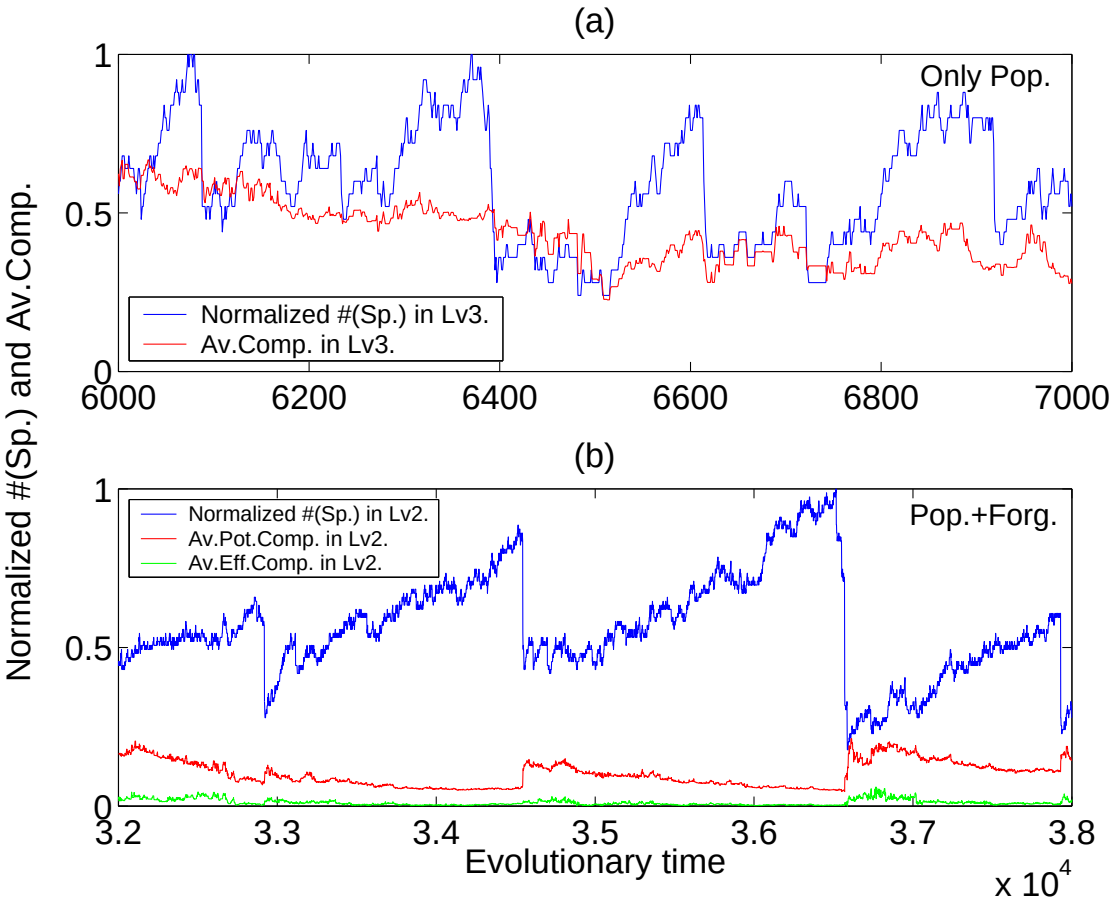


Figure 5.16: Zoom into the time evolution of the number of species and of the average competition strength (a) in level 3 for the model without adaptive foraging and (b) and in level 2 for the model with adaptive foraging.

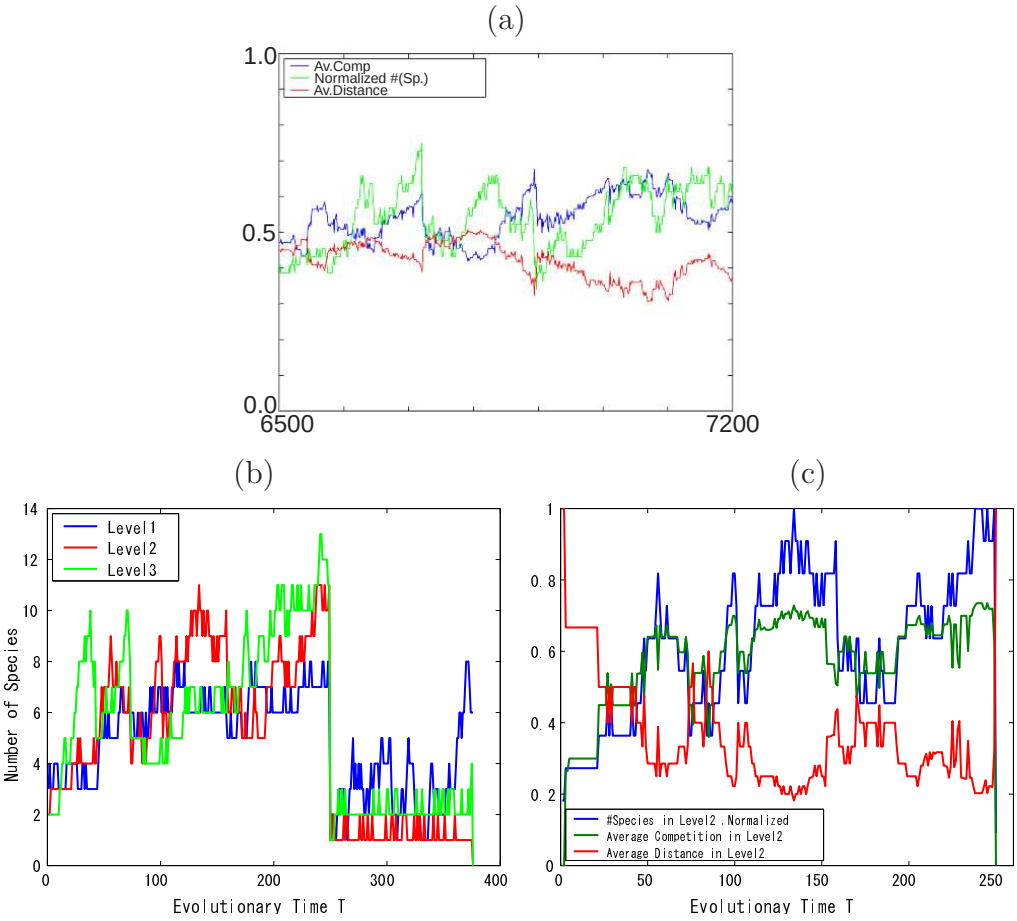


Figure 5.17: Other examples of the model without foraging dynamics. (a) With the parameter set $R = 1000, \alpha = 1, \beta = 1$ and $\sigma = 0.8$. The number of species divided by the maximal number of species in the time series in level 3 (green line), average competition (blue line) and average distance of species are plotted. (b) and (c) are obtained with Holling type II functional response. (b) shows the number of species in the three levels (level1: blue line, level 2: red line, level 3: green line), and (c) the number of species in level 2 (blue line), the average competition (green line) and the average distance of species (red line). The parameter values are: $R = 1000, \alpha = 1, \beta = 1$.

Chapter 6

Summary

We summarize the conclusions of this dissertation. We investigated the stability and structure of model food webs with up to three types of dynamics: dynamics for adaptive foraging and predator avoidance, population dynamics and evolutionary dynamics, and demonstrated that model food webs with adaptive behavior show different (sometimes opposite) outcome to model food webs without adaptive behavior. Our main findings are:
(1) The foraging dynamics with linear constraints strongly restricts effective link structure: the number of activated links between a set of species and their prey must be smaller than the sum of the predators and the prey.
(2) Investing in predator avoidance behavior in the model with linear constraints does not pay off, consequently all the species concentrate on foraging behavior.
(3) If nonlinear constraints on the foraging efforts are adopted, the restrictions (1) and (2) do not apply any more, but the stabilizing effect is still present. Nonlinear constraints on the foraging efforts are more realistic and better compatible with empirical data.
(4) Model food webs without adaptive behavior show negative "stability-complexity" relations under population dynamics, i.e., more links or more species imply a larger probability of a species becoming extinct.
(5) For the population dynamics with adaptive behavior, we find positive "stability-complexity" relations if "complexity" is measured by the average number of potential prey per species. However if interspecific competition based on potential links is taken into account, we again obtain negative "stability-complexity" relations.
(6) If the interspecific competition is defined by effective links, which includes the effect of niche differentiation, there are no mathematical restrictions on the effective link structure. But numerical simulations show that the effective connectance in this case is also low and positive "stability-complexity" relations are recovered.
(7) We investigated analytically the stability of fixed points of the dynamics and found a condition under which the positive fixed point is locally or globally stable. The condition applies to the topology of food webs and work for Lotka-Volterra type functional response with and without foraging dynamics. In both cases, the absence of omnivore or the perfect ecological efficiency makes the system stable.
(8) In terms of the local stability, the condition applies only to the effective link structure for webs with adaptive foraging.

(9) Intraspecific competition stabilizes fixed points for the model with and without adaptive foraging.
(10) Model food webs without adaptive foraging are unstable under evolutionary dynamics, i.e., they collapse after some time regardless of the details of the model, and the resulting food webs have only one trophic level. Thus a complex food web cannot be produced or sustained by the model.
(11) Incorporating adaptive dynamics into the evolutionary model stabilizes food webs: food webs persist in time under evolution and resulting food webs have several trophic levels. But the structure of webs is not realistic.

Adaptive behavior is one of the factors that change the energy flow in food webs and stabilize them. It is known that there is a link between physiological quantities such as the respiration rate or the maximum reproduction rate of organisms and their body size (or body weight). Thus the body size also affects the energy flow in food webs. Recently, it is suggested that the body size structure of natural food webs (Woodward et al., 2005; Brose et al., 2006a) has important implications for the stability of prey-predator interactions (Weitz and Levin, 2006) and complex food webs (Brose et al., 2006b). Together, adaptive behavior and body size structures, may account for more of the stability of complex natural food webs. It is actually reported that an evolutionary model based on the niche model together with adaptive behavior and the body size effect produces more realistic complex food webs (Guill and Drossel, 2008).

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Erklärung zur Dissertation gemäß § 9 Abs. 1DPO/AT

Hiermit versichere ich, die vorliegende Doktorarbeit ohne Hilfe Dritter nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus den Quellen entnommen wurden, sind als solche kenntlich gemacht worden. Diese Arbeit hat in gleicher Form noch keiner Prüfungsbehörde vorgelegen.
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